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THE BIOLOGY OF COELOIDES DENDROCTONI CUSHMAN (HYMENOPTERA-BRACONIDAE) AN IMPORTANT PARASITE OF THE MOUNTAIN PINE BEETLE (DENDROCTONUS MONTICOLAE HOPK.)

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Within recent years more and more attention has been paid to the value of parasites in the control of introduced insect pests, and several outstanding examples of biological control have been secured by the introduction of the native enemies of the host. Little or nothing is known, however, from an experimental or controlled basis, of the value of native parasites on indigenous hosts.

Barkbeetles in the last decade have destroyed millions of mature pines in Washington, Oregon, Idaho, Montana, California, and other western states, and hundreds of thousands of dollars have been spent by the federal government in combatting these outbreaks. Until very recently no attempt was made to preserve the beneficial insects during the treating of the trees infested with barkbeetles. This treatment consists of felling the infested tree, and either burning or peeling it, depending on the fire hazard, tightness of bark, and other factors. Whichever method used causes practically complete destruction of all subcortical life.

According to the studies of Volterra (1928) the destruction of host and predator in proportional numbers reduces the average number of the predator more than the average number of the host. Consequently, it seems of greatest importance to protect the predator as much as possible during control work.

Outbreaks of the mountain pine beetle are threatening the valuable commercial stands of western white pine in northern Idaho and have practically destroyed several fine lodgepole pine forests in Montana. In U. S. Forest Service Regions 1 and 4, approximately $817,900 has been spent since 1910 in efforts to control epidemics of mainly the mountain pine beetle.

Coeloides dendroctoni Cush. is the most important parasite of this scolytid in western white pine and lodgepole pine in these regions, and parasitism frequently runs as high as 80 or 90 per cent. A detailed knowledge of its biology and habits is consequently of great importance when so much control work is being done, as this knowledge can be used to prevent the destruction of the parasite by selective methods of control.

The data for the following study of the biology and habits[1] of this valuable insect were secured during the summers of 1928, 1929, and 1930, while the writer was employed by the U. S. Bureau of Entomology to investigate the biology and habits of the fauna associated with the mountain pine beetle.

The purpose of the study was (1) to determine the role played by the fauna associated with the mountain pine beetle; (2) to work out the biologies of this fauna; and (3) to correlate the present methods of artificial control with the seasonal histories of the beneficial fauna. With this knowledge it was felt that subsequent control operations could be carried out at a time when a minimum of beneficial insects would be destroyed, or could be conducted in such a way that the most heavily parasitized broods would not be treated.

The investigations for the lodgepole pine region were conducted chiefly near Sula, on the Bitterroot National Forest in western Montana. Sula is about 100 miles south of Missoula, at an elevation of about 5000 feet. The studies for the white pine region were made near Metaline Falls, Washington, on the Kaniksu National Forest. Metaline Falls is in the extreme northeast corner of the state at an elevation of about 2500 feet.

Acknowledgment is made to Dr. F. C. Craighead, in charge of the Division of Forest Insects, U. S. Bureau of Entomology and Plant Quarantine, for permission to publish these records. Acknowledgment is also made to Mr. J. C. Evenden, in charge of the field station, Coeur d'Alene, Idaho, A. L. Gibson, H. J.

[1]A study of the morphology of the larval form of the parasite can be found in the Jour. N. Y. Ent. Soc. 42: 297-317.

Rust, W. D. Bedard, R. L. Furniss, J. W. Johnston, and F. B. Foley, all of whom have assisted or given advice or both to the writer.

No previous studies have been made on this species, and no complete account is to be had of the biology of any representative of this genus.

BIOLOGICAL STUDIES OF THE GENUS *Coeloides*

Numerous authors have mentioned the hosts of the various species of *Coeloides*, but Xambeu (1898) was the first to give a brief account of its developmental stages and oviposition. Giraud (1872) gives a short note on *C. scolyticida* Wesm., Seitner (1924) speaks of *C. bostrichorum* Gir. as parasitic on *Ips typographus* L. He says that parasitism is greater in the upper portions of the bole where the bark is thinner. Taylor (1929) gives briefly the life history, habits, oviposition, and effectiveness of *C. pissodis* (Ashm.), a parasite of the white pine weevil. Schimitschek (1931) mentions *C. bostrichorum* Gir. parasitizing *Ips cembrae* and other barkbeetles. He gives a short account of its biology.

Before discussing the biology of the parasite a brief account of the seasonal history of its host seems worth while.

SEASONAL HISTORY OF THE HOST

Lodgepole Pine.—The mountain pine beetle begins to attack healthy trees the middle of July and continues to attack during most of August. The first eggs are laid within a week after the beetles have constructed the first few inches of their egg galleries. The eggs hatch after about a ten-day incubation period and the larvae feed until cold weather sets in. They continue feeding the following year until the middle of June and early July, when they begin to pupate. The pupal stadium occupies about two weeks. After transformation the callow beetles remain under the bark for varying periods but practically all emergence from the dead trees is over by the middle of August.

Western White Pine.—The seasonal history in white pine is more involved (De Leon, D., W. D. Bedard, and T. T. Terrell, 1934), and for the sake of clearness will be discussed with the seasonal history of the parasite.

SEASONAL HISTORY AND BIOLOGY OF *C. dendroctoni* IN LODGEPOLE PINE

The seasonal history of *Coeloides dendroctoni* is rather complicated (Fig. 1). A few adult parasites, not over five per cent of the total number, lay their eggs on the more advanced larvae of the mountain pine beetle during late August and September, a month or so after the attack of the beetle. After feeding three or four weeks, the larvae hatching from these eggs spin cocoons and overwinter as larvae within the cocoons. Pupation takes place the following May and June, and

the *Coeloides* adults emerge during the latter part of May and the first three weeks of June. But besides these adults which emerge from the trees still containing the larvae of the mountain pine beetle, another emergence occurs at the same time. This is from trees which were attacked by the beetle two years previously, and have been abandoned by the unparasitized brood for nearly a year. The parasites from these trees have remained as larvae within their cocoons for parctically

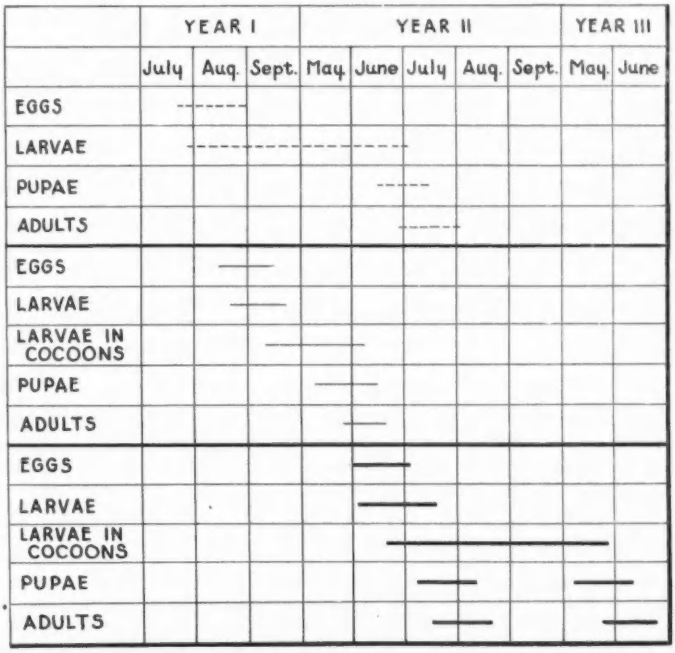

FIGURE 1. Seasonal history of *Coeloides dendroctoni* Cushm. in lodgepole pine, solid line; and general seasonal history of its host, *D. monticolae*, broken line. Thin solid line represents early generation; heavy solid line main generation. Chart represents parasitism as it occurs in one tree. October to April omitted, the insect being in cocoon during this period.

ten months. The parasites of this emergence make up fully 95 per cent of the total number of *Coeloides* that emerge during May and June. The females of both emergences lay their eggs on the larvae of the mountain pine beetle in the trees that were attacked the previous season. Though the parasitic larvae hatching from these eggs spin cocoons after feeding from three to five weeks, most of them remain as larvae within their cocoons until the following spring. They then pupate during May or early June for from 10 to 20 days, transform to new adults, and emerge in time to lay eggs upon the larvae of the mountain

pine beetle of the previous season's attack. Thus the chief emergence is again from trees attacked two years previously and which have been abandoned by the unparasitized mountain pine beetle for practically one year. That generation which develops on the beetle larvae the same season as the attack of the tree by the beetle has been termed the early generation; that generation which develops on the beetle larvae the June following the attack of the beetle has been termed the main generation.

There is, however, still another generation which is here called the summer generation. While probably about 95 per cent of the brood of the main generation overwinters, the remaining five per cent pupate very soon after spinning their cocoons; transform in about ten days, and emerge during the latter part of July and first part of August. An examination in the field, June 7, 1929, of 139 cocoons of *Coeloides* (spun in June, 1928) selected at random showed five empty cocoons from which emergence had occurred the previous season. This would mean an emergence of 3.6 per cent. Emergence from 500 cocoons spun in June, 1929, collected July 18, and kept under laboratory condition in a plaster of Paris container, showed a four per cent summer emergence. The first emergence occurred July 19. Emergence from 61 cocoons spun in June, 1929, and collected July 8, showed a 21.4 per cent emergence. The first emergence occurred July 18. This variation in data cannot be accounted for unless artificial conditions are the cause.

The larvae, cocoons, and adults of the summer generation are indistinguishable from those of the main, overwintering generation. The cocoons of the former are not found in localized groups, nor are they confined to the warmer sides of infested trees, nor does it appear that they are the progeny of the early generation.

Thus while the development of the principal brood requires practically a full year, there are two broods of *Coeloides* which together require slightly less than a year in which to develop.

In the field all of the cocoons spun in June, 1928, were found empty by June 17, 1929. As the first adult was secured May 21, it would seem that the period of emergence for *Coeloides* occupies about four weeks.

Egg Period.—The incubation period of 10 eggs kept under laboratory temperature ranged from 26½ hours to four days. Records of eggs laid in the field and left in the tree under natural conditions were difficult to obtain, owing to the fact that the bark had to be removed from over the larva on which the adult parasite was seen to work, in order to determine whether or not an egg had been laid and, if so, upon which larva. Frequently, examination revealed no eggs. Thus it seems likely that the adult may miss the larva with her ovipositor and not lay an egg; at all events it appears that no egg is laid, though the female may spend a half hour penetrating the bark. Two records secured in the field showed for one egg a period of 93 hours and for the other a period of 95 hours.

Feeding of Larvae and Cocoon Formation.—The young parasite on hatching crawls about over the surface of the beetle larva, which by

this time is thoroughly paralyzed, until it finds a suitable spot at which to feed. The parasite larva may be found on any part of the beetle larva except the head capsule, through which it does not feed; it may occur on the dorsal, ventral, or pleural regions, cephalad as well as caudad. The *Coeloides* larva has only vestigial mouth parts, of which the best developed are the mandibles; with these it apparently punctures the cuticle, sucking up the fluid that exudes therefrom. As soon as feeding begins the growth is rapid, especially in width; consequently, instead of being elongate with nearly parallel sides, it appears swollen after about eight to ten days, and with the segmentation less distinct. As the parasite larva matures, small, whitish "fat bodies" develop beneath the cuticle. The earliest recorded appearance of these is three days after hatching, but this is unusually early. When the larva is nearly mature the urate cells often assume a slight yellowish cast, as does the rest of the larva. Usually, when this becomes marked the parasite larva ceases feeding within a few days. It may spin a cocoon immediately, as is commonly the case; or it may delay doing so, for some as yet unknown cause, for an indefiinte period. The shortest recorded period elapsing from the time the egg was laid until a cocoon was spun was 15 days, but larvae under nearly identical conditions were found which did not spin cocoons after 80 days, though no feeding had been done during the preceding 55 or 60 days.

By the first week in July a great majority of the larvae of the parasite have spun cocoons. These may be divided into two groups, (1) those that are nearly white and (2) those that are rather tan-colored, but the two colors appear to have no significance. Cocoons of both colors are found side by side; males and females emerge from either, and both types contain overwintering larvae.

The cocoons of the early generation are generally smaller than those of the main generation, probably because the larvae parasitized in the fall are considerably smaller than those parasitized in the spring, and thus the parasite larvae, having less to feed upon, are proportionately smaller.

Pupal Period.—The pupal stadium of the female was found to range from 11 to 22 days, with an average of about 17 days. The male pupal stadium ranged from 10 to 13 days.

Emergence.—In the field, the first males were observed May 21, 1929, nine days before the first female was seen, but indications are that the females are not always as tardy in emergence as this. During the first three weeks of emergence males were very numerous on trees containing the cocoons of the parasite; not infrequently as many as 12 to 15 male *Coeloides* would be found clustered with their heads at the center in an area that could be covered by a silver dollar. Investigation of every such instance disclosed a female *Coeloides* chewing her way out from the cocoon under the bark. Evidently there must be an extremely attractive and penetrating odor emanating from her. The female is fertilized immediately after emergence by one of the waiting males.

Oviposition.—After emerging the female flies to a tree attacked the previous August, now containing beetle larvae more than half-grown,

and then crawls over the bark surface "sounding" with her antennae for the larvae (very rarely parasite larvae have been found on pupae of *Dendroctonus monticolae*) beneath, which are detected, in all likelihood, by the vibrations caused by the mandibles scraping against the tree tissues when feeding. The parasite does not employ entrance, ventilation, or exit holes as a means of getting closer to the larvae or finding better going for her ovipositor, nor, in fact, does she ever see the beetle larva on which her egg is laid; nor would she, as experimentation has proved, lay her eggs on an exposed larva however long the two remained together.

When a suitable host is found the parasite raises the end of her abdomen until the ovipositor is in a vertical position. She then adjusts herself until the tip of the terebra is over the selected larva, sometimes spending several minutes before she appears satisfied with her position, at other times but a second. Next a slight vertical vibration of the abdomen occurs as the ovipositor is worked into the bark. When the female reaches the host she depresses the terebra suddenly, forcing it, perhaps, through the cuticula of the larva. If this is what happens, it is not, however, to lay the egg within the larva, since the egg is deposited only on the surface of the larva, frequently even upon the head capsule. The precise time that the egg is deposited could not be determined. The length of time required to penetrate the bark probably varies with its thickness, texture, and moisture content; 12 minutes was the shortest time observed, and 50 minutes the longest. Immediately after the sudden depression of the terebra, mentioned above, the female withdraws it, usually wipes it off with her hind legs, and goes in search of another victim.

Effects of Oviposition.—The victims selected appear to be the larger larvae and there are strong indications that the parasite concentrates on the last or the last two instars. However, data at present are insufficient to warrant a positive statement in regard to this point. Though it shows the effect of oviposition after four or five hours, a parasitized beetle larva, within two days after the egg has been laid, becomes inactive and appears as though paralyzed, or at least stupified. When stimulated by some object such as forceps, it either shows no sign of life or moves only slightly and ceases movement much sooner than a non-parasitized larva that has been similarly stimulated. After about three days the larva usually shows no sign of life and is probably dead. In other respects, except for a very slight darkening of the tissues, the parasitized larva does not differ in appearance from a non-parasitized one until a great deal of the larval fluid has been sucked out by the parasite, causing the cuticula to collapse. Whether the appearance referred to is caused by the parasite piercing the larva and injecting a paralyzing fluid, or whether it is due to the mechanical effect of the puncture alone, has not been determined conclusively.

Experimentation has demonstrated that the piercing of the cuticle of a mountain pine beetle larva with a fine needle tends to produce the same effect as the piercing of the cuticula with the *Coeloides* ovipositor; but the larva pierced by a needle frequently blackens, and in many cases shrivels, after a few days. On the whole, the needle-pierced larva do not remain in a state of preservation as well as the larvae that

have been parasitized or larvae that have been punctured mechanically by taking the ovipositor of a freshly killed *Coeloides* and forcing it through the cuticula of the larva. To perform the puncturing operation it is necessary to cut off about one-half of the ovipositor of *Coeloides*, as the terebra of natural length is too flexible to pierce the cuticula of the beetle larva with ease. That portion of the ovipositor remaining attached to the body is the part used in the operation, and on the tip of it there generally appears a globule of colorless liquid, but whether or not this fluid is the element that causes this better state of preservation among the *Coeloides*-pierced larvae has not yet been determined.

It is probable, however, that a fluid is injected, for though the larva at the time of oviposition is only paralyzed it later dies as mentioned above. It may be necessary, for the development of the larva of the parasite, that there should be no decomposition of the host, and as the larvae parasitized by the adult *Coeloides* appear to remain in a state of preservation, it seems likely that the fluid injected not only kills the larva but also acts as an embalming or preserving fluid. It is general knowledge that certain other hymenopterous insects sting their prey and either paralyze them or kill them outright. In those killed outright it is possible that the fluid used may also act as an embalmer, though the studies of the Peckhams (1898) show that the larvae of many of the solitary wasps develop as well on decomposed caterpillars as on fresh ones.

Parthenogenesis.—A few experiments were tried to determine whether the females could reproduce parthenogenetically. Females reared from isolated cocoons were placed with bark containing larvae of the barkbeetle. No eggs were found on these larvae and the females showed no interest in the bark as did fertilized females which oviposited under similar conditions.

Thus it would seem that *C. dendroctoni* can not reproduce parthenogenetically and the fact that the males seem to be strongly attracted to a female emerging from the bark lends support to this belief.

Longevity of Adults.—Adult *Coeloides* collected in the field have been kept alive in captivity on sugar solution from 16 to 32 days, but the average number of eggs laid by an individual each day has not been determined. Ten eggs are the most that have been dissected from one female, though they probably produce many more.

SEASONAL HISTORY OF *C. dendroctoni* IN WESTERN WHITE PINE

Beacuse of the overlapping in the development of *D. monticolae* in western white pine, as pointed out under the heading, "Seasonal History of Host," the separate broods of the beetle and each period of parasitism will be followed through according to the time of parasitism, but the grouping of the attacked trees will be kept as given in the article by the writer and his associates on the biology of the mountain pine beetle (*loc. cit.*).

GROUP II. The first *D. monticolae* attack of the season occurs in June but the trees attacked are small in proportion to the number

of trees attacked in July and August. The brood of this attack develops rather rapidly and by the first week in July some of the brood is well enough advanced for parasitism by *Coeloides*. By the end of July most of the brood is well developed and by the middle of August most of it is in the pupal stage. Towards the end of August many of the callow adults are present and of these over half may emerge before the middle of September; the remainder stay under the bark until the following spring. The parasites begin laying eggs on the larvae of *D. monticolae* in this type of tree about the first week in July; parasitism continues until the brood of the beetle has reached the pupal state, after which it practically ceases, as pupae are rarely parasitized. Most of the developing parasitic larvae have completed feeding and spun their cocoons by the middle of August. Some of these (about 20%) pupate immediately after spinning their cocoons; transform to adults, and emerge the latter part of August. The rest of the brood of *Coeloides* remains in the larval stage within their cocoons until the following spring, when the larvae pupate, transform, and emerge during May and June.

GROUP III. The main beetle attack begins the first ten days in July, and attacks continue to occur to the middle of August. As the new attacks are practically continuous, the brood of the beetle can be found in almost all the larval stages after a period of about four weeks has elapsed, and towards the middle of August pupae and rarely callow adults can be found in the earliest attacked trees. The middle of September finds these trees with some callow adults under the bark, and while it is possible that a few of these emerge, indications are that they compose less than one per cent of the brood. Thus, separate trees of this type contain overwintering brood in stages of development from probably the egg to the callow adult.

The female parasites begin to oviposit on the developing *D. monticolae* larvae about the first of August. The developing parasitic larvae finish feeding and spin cocoons usually before cold weather sets in. In some cases it seems possible that a few *Coeloides* larvae may overwinter without spinning cocoons and spin them instead the following spring. Naked larvae of *Coeloides* have been found in early spring, though it was not determined whether they later spun cocoons. A few larvae, probably developing from the first eggs laid, pupate immediately after spinning their cocoons and emerge as adults from their cocoons within a week or two after pupation. Data indicate that the amount of brood which emerges the same season as the cocoon is spun is less than three per cent. The remainder of the brood overwinter in their cocoons in the larval stage; the larvae pupate in the spring and emerge during May, June, and the first part of July, depending chiefly on the exposure. About a 20 per cent parasitism was found to occur in trees attacked by *D. monticolae* in July.

Brood of *D. monticolae* in trees attacked after the first of August remained for the most part too small for parasitism by *Coeloides* that season. Parasitism in August attacked trees was found to be about two per cent, and all the cocoons were found to be occupied.

GROUP I. Parasitism of the brood of *D. monticolae* the same season as the attack is represented by Groups II and III. Group I represents parasitism of the brood of *D. monticolae* the spring following the beetle attack. In this type the parasites work chiefly on the trees that have been attacked by the mountain pine beetle the previous August and September. Since the brood in these trees, as mentioned previously, overwinter in the small larval stage, it is, by the time the *Coeloides* have emerged from their cocoons, far enough advanced for parasitism. Some parasitism of the brood of the beetle no doubt occurs also in the trees attacked the previous July, for though most of the brood is in the callow adult stage by the time the *Coeloides* are abroad, a few *D. monticolae* larvae are probably present.

All the larvae of *Coeloides* in Group I have completed development and spun their cocoons by the middle of July. Some of these remain as larvae within their cocoons until the following spring, then pupate, transform to adults, and emerge; others pupate, transform and emerge as adults within six weeks after spinning their cocoons.

The brood of the beetle not parasitized developed to where by the end of July over 90 per cent of them were in the callow adult stage. The callow adults begin to emerge about the end of the first week of August and continue the main summer attack of the mountain pine beetle. However, a few of the callow adults, for some undetermined reason, still remain in the trees; some beetles were found September 15 (the date of the last examination) in trees from which most of the beetles had emerged during August.

In each of the last two types distinguished above, one finds an irregularity in distribution of parasitism. Some trees of each of these two types are heavily parasitized; often parasitism as high as 80 to 90 per cent is found, but other infested trees nearby the heavily parasitized trees show a very small per cent of parasitism, for some as yet unaccountable reason.

Parasitism in a Group III tree was fairly high, but not enough observations were made on this type to determine whether the parasitism was equally heavy among other similar trees.

BIOLOGY AND HABITS OF *C. dendroctoni* IN WESTERN WHITE PINE

It was very much more difficult to secure oviposition of *Coeloides* in the eastern Washington type than it was in Montana. Only five eggs were secured and none of these hatched.

No exact records were kept in this type on the development of the larvae. The time of cocoon formation generally occurs three to four weeks after the eggs have been laid. The males appear two to three days before the females. The males from lodgepole pine infested with the barkbeetle were also found to emerge earlier than the females. It was believed at that time that the earlier emergence of the males was the result of a more rapid developmental rate of the male pupa, or to an ability to pupate earlier in the season, but it was found that generally there is very little difference in the pupal stadia between the two sexes, so that some other factor, such as that the males remain a

shorter time in their cocoons after transformation than do the females, may be the cause of the difference in time of emergence.

During the spring of 1930 the first adult, a female, was found May 12 on a plot of open exposure; on May 14 the parasites, chiefly males, were fairly common on the bark of infested trees in the same locality. The following weeks clusters of males were frequently observed on the bark of trees infested with the barkbeetle waiting for the female to emerge. From this time on to the middle of September *Coeloides* adults could be found on infested trees.

The period of emergence appears to be due to a great extent to the exposure of the trees containing the cocoons. Emergence up Pass Creek, which is in a rather deep canyon, was almost a month behind an exposed flat where a good many examinations were made.

SECONDARY PARASITES

Two hymenopterous insects, *Eurytoma n. sp.* (Eurytomidae) and *Gelis* sp. (Ichneumonidae), were reared from the cocoons of *Coeloides dendroctoni* in lodgepole pine in Montana.

During the season of 1928–29 *Eurytoma n. sp.* parasitized about eight per cent of the larvae of *Coeloides*. *Gelis* sp. was rare; only four males and two females were reared from 874 cocoons of *Coelides*. Nothing was learned of its habits. Some notes on the habits and seasonal history of the former species are in preparation.

No secondary parasites were secured from over 1500 cocoons of *C. dendroctoni* collected in western white pine in eastern Washington. Only a few adult *Eurytoma* were observed in this region. It has been observed ovipositing in trees containing larvae of *Coeloides*, and two larvae and one pupa were collected from the larval galleries of *D. monticolae*, but beyond this no other data were secured for *Eurytoma* in this locality.

ECONOMIC STATUS OF *C. dendroctoni*

The most important parasite of the larval stage of *Dendroctonus monticolae* in lodgepole pine in the region of Sula, Montana, is *Coeloides dendroctoni* Cush. Parasitism in some trees often runs as high as 95 per cent, but on an average the importance of *Coeloides* seems to vary with the length of time an infestation has been present on an area. Where *D. monticolae* has been present for the shortest time, as in the outlying groups of trees, parasitism by *Coeloides* has been found the lowest. This is probably due to a number of factors. The *Coeloides* found generally over the forest in *Ips*-infested, windthrown, snow-broken, and otherwise damaged trees, infested with barkbeetles, are probably insufficient in numbers the first year or two after *D. monticolae* arrives to parasitize a large percentage of them. A second factor is related to the life history of the parasite. The main generation of *Coeloides* remains in the trees killed nearly a year after their host, *D. monticolae*, has left. By the time the adults of this parasite have emerged at least the van of the main body of the infestation has left them behind, and it is not unlikely that instead of "catching up" with the *D. monticolae* in the outlying groups they will concentrate

chiefly on the insects infesting nearby trees. Such action would prevent heavy parasitism of *D. monticolae* in the outlying groups until these groups have become practically a part of the main body of the infested stand. It is thought that a combination of these two factors, (1) small numbers of parasites present when *D. monticolae* enters an area, and (2) slowness of the parasite in "catching up" with its host, are partly responsible for the low parasitism in the outlying groups.

Inability to multiply rapidly is thought to be another factor that prevents the rapid increase in parasitism in any area. As the female *Coeloides* dissected did not have more than 10 mature or nearly mature eggs in its ovaries, it is probable that they do not lay many eggs a day. Laying, as she does, but one egg on each beetle larva, the female parasite must expend a great deal of time and energy for each egg laid. Added to this handicap is the fact that the parasite has but one main generation a year.

These handicaps seem to have prevented the parasite from becoming more important as a controlling factor.

APPLICATION OF SEASONAL HISTORY TO ARTIFICIAL CONTROL

Lodgepole Pine.—The value of these observations on parasitism lies in the fact that they indicate that where partial control is possible we should be able to favor the increase of this important parasite by confining control work to the more recently established parts of an infestation and to the fall of the year. On the other hand, if control work for the entire area of the outbreak is possible, confining the work to the fall would probably make this parasite much more effective in controlling the brood in the trees inevitably missed in any large control operation, since control in the fall would kill all of the brood of *Dendroctonus monticolae* and leave practically all the emerging *Coeloides* to work on the infested trees missed in the treated areas.

There are several other advantages that fall control has over spring control besides that of preserving the brood of *Coeloides dendroctoni* Cush. These are the advantages of having better roads over which to haul in men, supplies, and equipment, less fire hazard, and more settled weather conditions. Spring control is begun during April or early May, when at high altitudes the roads are soft from thaws, if snow is not still on the ground; when the streams are high, and when there are chances of severe snowstorms. All these factors tend to reduce to a minimum the efficiency of a control project, and when many thousands of trees are to be treated, any lessening in efficiency slows up the work and greatly increases the overhead expenses.

Taking all points into consideration, fall control of infested trees has everything in its favor and spring control little, if anything, in its favor.

Western White Pine.—Unquestionably, *Coeloides dendroctoni* is the most important parasite of the mountain pine beetle in white pine as well as in lodgepole pine. However, the irregularity of parasitism, which may be owing to the overlapping in the development of the *D. monticolae* brood, makes it very difficult to recommend a time for

artificial control of the brood of the beetle that will not also destroy a good many parasites. If it were possible to treat the infested trees within three to four weeks after the beetle attack, few *Coeloides* would be destroyed. However, as the main attack extends from early July to the first part of September, such treatment would be impractical. The best policy to follow would be to treat the infested trees at a time when it can be done most economically and to leave the trees with very heavy parasitism standing, somewhat like seed trees are left in a cutting area. Trees falling in the category of Groups I and II for the time of parasitism are the most heavily parasitized.

Mr. Bedard, in an unpublished report, has shown that the mortality of *Coeloides* in their cocoons after the bark has been peeled in control work is very great, so that this method of control cannot be expected to protect the parasites.

OTHER HOSTS

Coeloides dendroctoni Cush. was also found to parasitize the larvae of *Ips vancouveri* Sw., *Ips oregoni* (Eich.), and *Orthotomicus caelatus* (Eich.). It was found to attack the brood of the mountain pine beetle in white-barked pine (*Pinus albicaulis* Engel.), but it does not parasitize this beetle in western yellow pine (*P. ponderosa* Laws.).

SUMMARY

Coeloides dendroctoni Cushman, a solitary braconid, is the most important parasite of the mountain pine beetle (*Dendroctonus monticolae* Hopk.) in lodgepole pine in western Montana and western white pine in eastern Washington and Idaho. It is not known to attack the mountain pine beetle in western yellow pine. Average parasitism ranged from about four to 32 per cent, depending on the age of the infestation, but in individual trees it frequently reached 90 per cent.

The life cycle of *Coeloides dendroctoni* Cush. ranged from about four weeks to nearly a year. The principal emergence of the parasite and parasitism of the brood of the mountain pine beetle occurred during June. Most of the parasitic larvae overwintered, but some pupated immediately after feeding was finished and emerged during July and August. There was also some parasitism of the brood of the beetle during August and September.

Descriptions of the developmental stages and notes on the habits of the adults are given.

Two secondary parasites, *Eurytoma* n. sp. and *Gelis* sp., were reared from the cocoons of *Coeloides dendroctoni* Cushman in Montana. No secondary parasites were found in eastern Washington.

The apparent reasons for the low efficiency of *Coeloides dendroctoni* Cush. are given, and a time for artificial control of the brood of the mountain pine beetle in lodgepole pine is recommended whereby relatively few of the brood of its parasite will be injured. In white pine it is recommended that during control operations trees most heavily infested with the parasite be left untouched, something like seed trees are left after a clear cutting logging operation.

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THE BIONOMICS OF ENTOMOPHAGOUS COLEOPTERA, by W. B. Balduf. (Planograph), pp. 1–220, 108 text figures, cloth bound. 1935. Published by John S. Swift Co., Inc., 105 S. Ninth St., Saint Louis, Mo. Price, $4.50.

This work is divided into fourteen parts each of which treats a family or a group of related families. It gives us a consistent picture of the general usefulness of Coleoptera as predators on other insects. More and more. various students of biological control of insect pests are realizing that in the great hordes of predaceous insects man has coworkers in the control of pests which in many ways are as valuable as the so-called parasitoid insects. Besides this view given by the author the volume is a key to the literature. The bibliography is divided into sections, one for each family treated in the text. Further usefulness is achieved by a thirty-five page, two-column index.

In American entomological literature we have numerous short papers on the habits of species or limited groups but we have few compilations on the habits of the species of an Order or large section of an Order of insects. Because of the great richness of the North American fauna we are still describing new species. We are glad to see the turn in the science come when a worker in touch with one of the great libraries of this country (The Library of the Illinois State Natural History Survey) feels warranted in taking time to compile such information as is summarized in this volume. The author's name will not be widely advertised two hundred years from now because it is on a thousand new species of insects. Instead he has at a sacrifice of research time given us a very useful organization of an otherwise chaotic area of the science. The European literature on entomology is rich in volumes of this type. Such works are useful in teaching entomology and always stimulate further work in the field covered as they indicate the gaps in our knowledge of the subject. These unknown areas can then be attacked directly and cleared up.

The Editor has grown up in the age of type and typesetting and suffers from a certain nervous shock whenever another volume appears in mimeograph or some one of the photographic variations of this typewriter process. M, W and low case e still clog and come out too black. However, this book is remarkably well printed. The numerous line and stippled illustrations are as well reproduced or even better than are many zinc etchings in current entomological journals. Excellent paper is used. The volume is a credit to the printer as well as to the author.—C. H. K.

THE RELATION OF CERTAIN FUNGI TO LARVAL DEVELOPMENT OF EUMERUS TUBERCULATUS ROND.

(Syrphidae, Diptera)

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With the expansion of the narcissus-bulb industry during the past few years, bulb flies have become pests of increased importance, and many investigations have been directed toward their control (11). Two lesser bulb flies infest bulb plantings, the one most commonly found being *Eumerus tuberculatus* Rondani. A few years ago the *Fusarium* basal-rot disease also became prevalent in narcissus bulbs, especially in the eastern part of the United States, and it was soon observed that bulbs severely affected with this disease were invariably infested with larvae of *E. tuberculatus*, (Plate I). A study of the relation of this insect to the basal-rot *Fusarium* was therefore undertaken at Babylon, N. Y., and later was expanded to include observations on other bulb-infesting fungi.

As early as 1920, according to Collin (4), opinions were divided "as to whether the larvae are primarily responsible for the destruction of the bulbs, or whether they only attack those bulbs which have begun to decay from other causes." Broadbent (3) in 1925 suggested that larvae of *Eumerus strigatus* Fall, another lesser bulb fly closely related to *E. tuberculatus*, are frequently associated with decaying or fermenting bulbs of narcissus and onions, although she stated that the females deposit their eggs in sound bulbs and that the larvae are equipped with strong mouth hooks capable of tearing healthy plant tissue. Hodson (7) concluded from his experiments that the larvae may gain entrance to healthy bulbs and destroy them.

Ensign's paper (5) on the investigations of J. G. Leach on the relation of seed corn maggot (*Hylemyia cilicrura* Rond.)

[1]Acknowledgments are made to Dr. C. A. Weigel, under whose general supervision this study was made, for his suggestions and interest in the work, and to F. S. Blanton, for identifying all flies used in the investigation.

to the black-leg disease in potatoes suggested to the junior author the possibility that some similar relationship might exist between *Eumerus tuberculatus* and the various bulb rots. The value of investigating the association of the fly larva with the host plant as a food medium was recognized. Doucette, in April 1926, made a few tests in rearing larvae in agar, but he did not attempt to keep the cultures free from contamination, as his object was merely to work out the several larval stages. However, Martin (9) noted, in work done in 1929, that larvae develop more rapidly on decaying bulb tissue than on healthy macerated bulb tissue.

In the summer of 1930 Spruijt and Huff carried out preliminary studies with larvae in pure culture medium of cooked bulbs with agar, and found that larvae hatched from surface-sterilized eggs developed very poorly on bulb-agar alone but grew rapidly when the basal-rot *Fusarium* was introduced.[2] This work involved only a limited number of larvae, but it showed that there is a nutritional relationship between larval development and the presence of the basal-rot *Fusarium* in the medium.

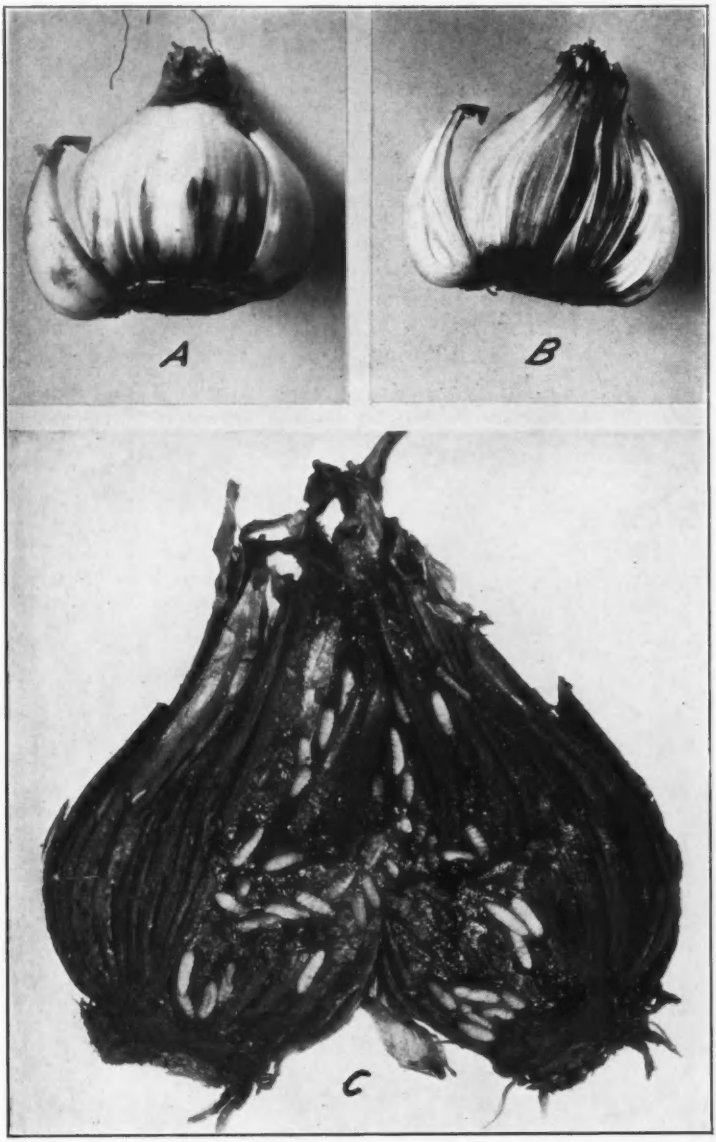
More detailed investigations concerning the relationship between the larvae of *Eumerus tuberculatus* and its food were initiated in the summer of 1931, and the results are reported in this paper.

METHODS

Obtaining larvae free from microorganisms.—In order to determine the effect of the presence of certain fungi and bacteria upon the growth of larvae, it was desirable to obtain them free from other organisms. This was accomplished by sterilizing the surface of the eggs in a solution of calcium hypochlorite[3] and allowing them to hatch in a sterile environment. The eggs were immersed in the solution for 1 to 2 minutes, removed one at a time with a sterile needle, and each was placed without being washed on a slant of sterile agar, where it was allowed to hatch. When this work was carefully done, no fungi or bacteria developed in the tubes of nutrient agar containing the larvae. All the eggs used in obtaining larvae for this work were laid by flies in captivity that had been identified as *Eumerus tuberculatus*.

[2]Unpublished notes.

[3]Calcium hypochlorite solution was prepared according to a modification of Wilson's method (Wilson, J. K. Calcium hypochlorite as a seed sterilizer. Amer. Jour. Bot. 2: 420–427, 1915) as follows: 10 grams of commercial chloride of lime (28 per cent Cl) was stirred into 140 cc. of distilled water. After standing for an hour or so, the liquid was decanted and passed through filter paper. The solution was used immediately or stored in a stoppered bottle. No solution older than two weeks was used.



Rotted narcissus bulbs: A, Outside of a bulb affected with the *Fusarium* basal-rot disease; *B*, the same bulb cut longitudinally, showing rotted basal plate and scales; *C*, rotted bulb infested with larvae of *Eumerus tuberculatus*.

Preparation of media.—All media used in this study were prepared from healthy Victoria narcissus bulbs, since this variety is very susceptible to the basal-rot disease and fly infestation. Three types of media were used, namely, surface-sterile tissue, autoclaved tissue, and bulb-agar.

Two methods were employed in preparing the surface-sterile-tissue medium. One consisted of removing all soil and dried scales from the bulbs and surface-sterilizing them for 1 hour in a 0.1 per cent solution of mercuric chloride; under aseptic conditions pieces of tissue were then taken from the inner portions and placed in test tubes on sterile plain agar slants. The other method consisted of removing pieces of tissue from the inner portions of bulbs with a sterile scalpel, surface-sterilizing them in a solution of calcium hypochlorite for 5 minutes, and placing them, without being washed, on sterilized plain agar slants. In each case the tubes were set aside for a week or more to make certain that they were free from microorganisms before larvae were introduced.

The autoclaved tissue was prepared by placing an elongated piece of healthy bulb tissue with 3 or 4 cc. of melted plain agar into each of a number of test tubes and autoclaving at 15 to 20 pounds' pressure for 30 minutes.

Bulb-agar was prepared as follows: Five hundred grams of bulbs were cleaned and the dead scales removed. They were then cut in half longitudinally and cooked in 1 liter of water until soft. With care not to mash the bulbs, the liquid was poured through cheesecloth and enough water added to the extract to restore the volume to 1 liter. Fifteen grams of agar was added to the extract and the whole autoclaved for 30 minutes. This medium was used in the majority of the tests.

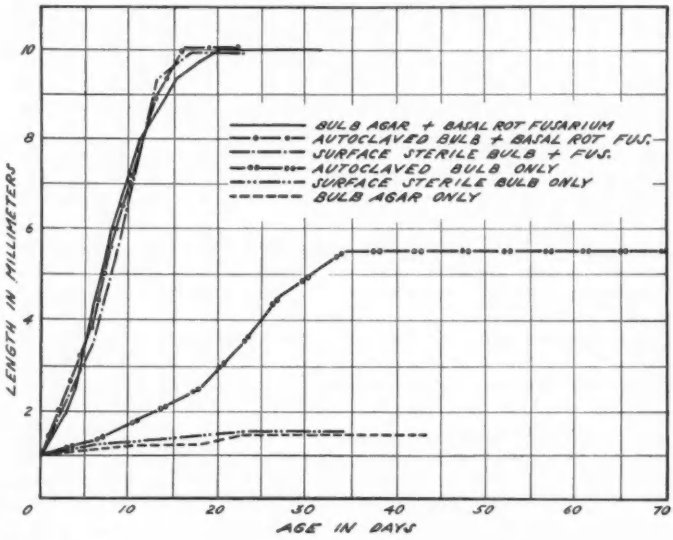
Rearing larvae and studying their development.—The larvae were reared in test tubes on various diets of sterile bulb media and pure cultures of various fungi and bacteria. They were all grown under the same environmental conditions in daylight at ordinary laboratory temperatures (68° to 77° F.). At the beginning of each test all the larvae were approximately 24 hours old and measured 1 mm. in length. In nearly all tests two or more series of 10 larvae each were used. Individual growth records were taken, and this necessitated rearing each larva in a separate tube. Increase in length was used as a criterion for growth. Measurements were made at frequent intervals (usually every 2 or 3 days) by laying a millimeter scale alongside of the tube. The dates of pupation, emergence, and death were also recorded. From these individual records the average rate of larval growth, duration of the larval period, age at pupation, and age at time of death were computed for each nutrient.

EXPERIMENTS

Larval growth in the presence, and in the absence, of the narcissus basal-rot Fusarium.—Parallel series of 40 larvae each were grown on the three types of narcissus-bulb media. Into half the tubes of each series a pure culture of the narcissus basal-rot *Fusarium* was introduced

when the larvae were 1 day old. The remaining tubes were kept sterile to serve as checks.

The larvae in the presence of the fungus grew rapidly and uniformly to a length of 10 mm. irrespective of the type of medium. (Text fig. 1.) With the fungus on surface-sterile and autoclaved tissue pupation occurred in an average of 6 days after the larvae attained this length, whereas on the bulb-agar more than twice as much time was required. Apparently normal adult flies emerged from all pupae, and the length of the larval period seemed to have no effect upon the length of the pupal period.

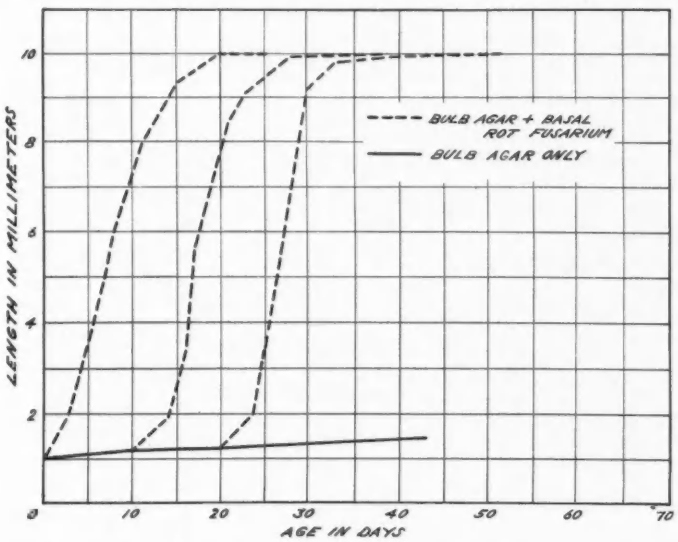


TEXT FIG. 1. Rate of growth of *Eumerus tuberculatus* larvae on different types of bulb media in the presence and in the absence of the basal-rot *Fusarium*.

Those larvae in the absence of the fungus developed very slowly, and most of them died before pupation. No larvae on bulb-agar or surface-sterile tissue in the absence of the *Fusarium* ever became more than 1.8 mm. long, and all died after a month or more. (Text fig. 1.) On the autoclaved tissue a few larvae were able to pupate and emerge as normal-sized flies, but the majority died before pupation. The few that did reach maturity were in the larval stage twice as long as those on the same medium in the presence of the basal-rot *Fusarium*. With the data at hand no explanation can be given concerning the differences in larval growth on the surface-sterile tissue and the autoclaved tissue in the absence of the fungus.

Another experiment was carried out which further emphasized the importance of the basal-rot *Fusarium* in larval nutrition. A 1-day-old

larva was placed in each of 40 test tubes containing slants of bulb-agar. These tubes were divided into 4 groups of 10 each. To one group the fungus was introduced immediately, to another it was not introduced until the larvae were 10 days old, to another not until 20 days old, and to the remaining group no fungus was added. None of the larvae in any group grew to more than 1.5 mm. in length before the fungus was introduced, but as soon as it was added they grew rapidly. (Text fig. 2.) From the time the fungus was added there seemed to be no significant difference in the rate of larval growth whether it was introduced when the larvae were 1, 10, or 20 days old. This partial starvation for 10 to 20 days had no visible effect upon the health of the larvae



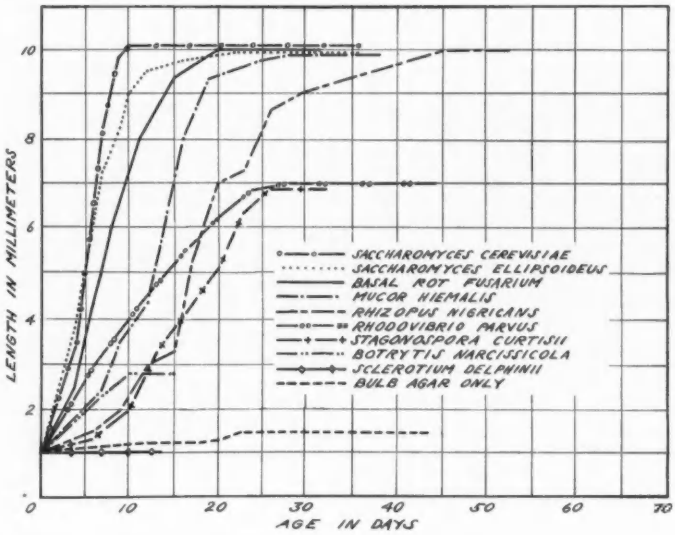
TEXT FIG. 2. Rate of growth of *Eumerus tuberculatus* larvae when introduction of the basal-rot *Fusarium* was delayed until the larvae were 10 and 20 days old as compared with the rate of growth when the *Fusarium* was introduced when the larvae were one day old.

after the *Fusarium* was added, but only a few adults emerged from pupae developed from these larvae.

These results show that larvae feeding in the presence of the narcissus basal-rot *Fusarium* develop more rapidly and attain a larger size than those fed on sterile bulb media alone.

Larval growth in the presence of other fungi and bacteria.—The majority of fly-infested bulbs are affected with the basal-rot disease, but it has often been observed that mechanically injured bulbs and bulbs rotted by other fungi, such as *Rhizopus nigricans* Ehr. and *Botrytis* spp., may also be infested. Since the basal-rot *Fusarium* proved to be so desirable in the diet of the larvae, it was suspected that other common

parasitic and saprophytic fungi might have a similar effect. This possibility was investigated by growing larvae on sterile bulb-agar in the presence of pure cultures of the following fungi: *Saccharomyces cerevisiae* Mayen, the American grain-distillery yeast; *S. ellipsoideus* Reess, var. Steinberg, the German white wine yeast; *Rhizopus nigricans* Ehr., the pathogene causing soft rot of narcissus bulbs; *Mucor hiemalis* Wehmr.; *Stagonospora curtisii* (Berk.) Sacc., the narcissus leaf scorch pathogene; *Botrytis narcissicola* Klebh., the narcissus "smoulder" pathogene; *Rhodovibrio parvus* (Molisch), a soil-inhabiting red bacterium; and *Sclerotium delphinii* Welch, which may attack the bulbs of narcissus and underground parts of many other plants.[4]



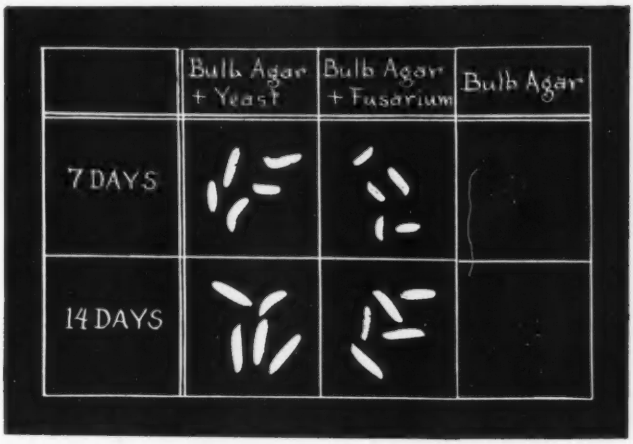
TEXT FIG. 3. Rate of growth of *Eumerus tuberculatus* larvae in the presence of various fungi and on bulb-agar alone.

Two series of 10 larvae each were employed for each fungus except *R. nigricans* and *M. hiemalis*, for which only one series of 10 larvae was used. The average rate of larval growth in the presence of each fungus was computed from individual growth records. (Text fig. 3.)

The results show that larvae in the presence of either species of yeast, *Saccharomyces cerevisiae* or *S. ellipsoideus*, develop more rapidly than those in the presence of the basal-rot *Fusarium*. (Text figs. 3

[4]Many thanks are extended to Dr. F. A. McDermott, of the E. I. du Pont de Nemours and Co., Wilmington, Del., for providing the two cultures of yeast, and to Nathan R. Smith, of the Bureau of Chemistry and Soils, U. S. Department of Agriculture, for identifying the red bacterium.

and 4.) With *Rhizopus nigricans* and *Mucor hiemalis* the majority of larvae pupated, but they developed more slowly than those in the presence of yeasts or *Fusarium*. The rate of development was still slower when *Rhodovibrio parvus* or *Stagonospora curtisii* was growing on the medium with the larvae. With the former the larvae made considerable growth at first, but with both these organisms nearly all died before pupation, and the few that did pupate produced adults that were about half the size of the normal flies. In the presence of *Botrytis narcissicola*, larvae developed slowly for about 10 days and then ceased feeding, and all died within 3 weeks. Those in the presence of *Sclerotium delphinii* made no growth and all died in less than 2 weeks. (Text fig. 3.)



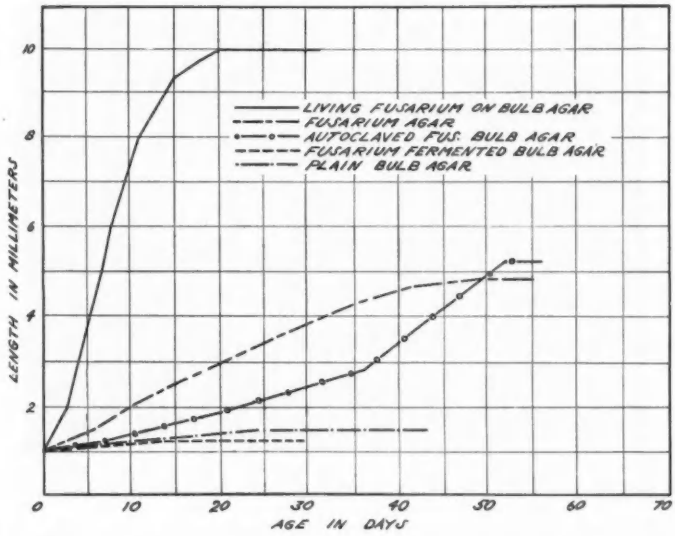
TEXT FIG. 4. Relative larval development of *Eumerus tuberculatus* on bulb-agar in the presence of yeast and *Fusarium* and on bulb-agar alone.

Nutritional relationship between the basal-rot Fusarium and the larvae.—An experiment was conducted in which larval development was compared on two types of agar media, one containing the basal-rot *Fusarium* and the other containing bulb extract in which the fungus had grown.

These media were prepared as follows: A pure culture of the basal-rot *Fusarium* was grown in 1-liter Erlenmeyer flasks containing 250 cc. of sterile bulb extract similar to that used in the preparation of the bulb-agar medium previously described. After 7 days the thick mycelial mat which formed over the surface of the solution was removed and placed in running tap water for 1 hour to remove as much of the extract as possible. After excess water had been removed by laying the mycelium on filter paper for several minutes, a 5-gram piece of the fungus mat was placed in each of several tubes together with 5 cc. of 1.5 per cent plain agar. The tubes were autoclaved and slanted.

This medium containing the killed *Fusarium* is called "*Fusarium* agar," since the only nutrient substance present was the killed fungus.

The bulb extract in which the fungus grew was freed from mycelium and spores by passing it first through several layers of cheesecloth, then through filter paper, and finally through a Berkefeld filter. A 1.5 per cent agar medium was prepared from the filtrate, and then tubed, autoclaved, and slanted. It is assumed that any fermentation or digestion products formed from the bulb extract by the activity of the fungus, other than those possibly destroyed by autoclaving, were included. This medium is called "*Fusarium*-fermented bulb-agar," since the fungus had grown in the medium for a week and caused some fermentation.



TEXT FIG. 5. Rate of growth of *Eumerus tuberculatus* larvae on sterile bulb-agar and on bulb-agar in the presence of living and killed *Fusarium* and of its substratum.

Three series of 10 larvae each were grown on *Fusarium* agar and two series of 10 each on *Fusarium*-fermented bulb-agar. Larval development on these two media as compared with that on living *Fusarium* on bulb-agar and on plain bulb-agar is shown in text fig. 5. On the fermented bulb-agar larvae were unable to grow to more than 1.5 mm. in length, and all died within 30 days. Larvae developed little better on this medium than on bulb-agar in which the fungus had never grown. On the other hand, considerable growth was made on *Fusarium* agar. (Text fig. 5.) At 48 days of age the larvae averaged 4.8 mm. in length, and several had attained 10 mm. The majority

lived for 50 days and a few for more than 3 months. However, all larvae died before pupation.

This brief experiment indicates, therefore, that the essential nutritional factor or factors are not present in the culture medium when the fungus is absent or, if present, is inactivated or changed by autoclaving. Since larvae were able to make noticeable growth on the medium containing the autoclaved basal-rot *Fusarium* as the only source of food, it appears that the essential nutritional factor or factors are present in the fungus and remain there, in part at least, after being autoclaved. However, when larval development on *Fusarium* agar is compared with that on bulb-agar plus the living *Fusarium*, it is clear that feeding on the killed fungus does not result in normal growth. (Text fig. 5.)

The results of another experiment offer an explanation for the difference existing between larval development on bulb-agar plus the living fungus and that on *Fusarium* agar. Cultures of the basal-rot *Fusarium* were grown in 20 test tubes containing bulb-agar. When the cultures were 7 days old, 10 of the tubes were autoclaved for 30 minutes at 18 to 20 pounds' pressure, and reslanted. Therefore, this medium contained the autoclaved *Fusarium* plus *Fusarium*-fermented bulb-agar. A 1-day-old larva was placed in each of the 20 tubes. Larval growth on this medium was similar to that on *Fusarium* agar, though a little slower (Text fig. 5), but the larvae were much inferior to those grown in the presence of the living *Fusarium*, indicating that the essential nutritional factor present in the living *Fusarium* was partially inactivated or changed by heat. The nature of this essential factor which seems to be contributed by the fungus has not been determined.

DISCUSSION

It is not new to science that fungi and bacteria play an important role in the nutrition of many insects. In 1908 Bogdanow (2), who was probably the first to attempt to rear flies free from microorganisms, reported that larvae of the flesh fly *Calliphora vomitoria* L. required the presence of certain bacteria for normal development. Guyenot (6) in 1913 showed that under aseptic conditions the larvae of the fruit fly *Drosophila melanogaster* Meig. (*D. ampelophila* Lŏw.) would not develop on foods free from microorganisms, but developed normally when yeasts were introduced. The findings of Guyenot were confirmed by Loeb and Northrop (8), Northrop (10), and more recently by Baumberger (1). Baumberger also studied the nutritional relationship of *Musca domestica* (the house fly) to manure, *Desmometopam nigrum* Zett. to decaying meat, and *Sciara sp.* to decaying wood, and found that all fed upon microorganisms growing in the substrata.

Many other references could be cited to show that larvae of the lesser bulb fly are not unique in using fungi in their diet.

Since bulbs in the ordinary course of production are not sterile, the experiments described above do not directly indicate the extent to which *Eumerus tuberculatus* may be of importance in bulb-growing sections, whether the insect plays a part in spreading fungi that would otherwise remain harmless, or whether control measures are needed.

SUMMARY

A study has been made of the relation of larvae of *Eumerus tuberculatus* Rondani to the basal-rot *Fusarium* and other fungi. Larvae free from microorganisms were obtained, and their growth was observed on diets of three types of sterile bulb media, namely, surface-sterile tissue, autoclaved tissue, and bulb-agar, with and without pure cultures of the basal-rot *Fusarium* and other fungi and bacteria.

It was found that on all these media the presence of fungi was necessary for normal development. In the presence of the basal-rot *Fusarium* all the larvae grew rapidly to maturity. When living yeasts were used in the diet in place of *Fusarium*, the larvae developed more rapidly and became slightly larger, and when *Rhizopus nigricans* or *Mucor hiemalis* was substituted, the larvae also developed to maturity. In the presence of certain other fungi and bacteria, however, the larvae made some growth but died before reaching maturity. When *Fusarium* was separated from the bulb and inactivated by autoclaving, the larvae were unable to complete their development. The results of this investigation indicate that the larvae of *Eumerus tuberculatus* require the presence of certain living fungi, together with the bulb media, in order to complete their normal development.

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WEEDS, by W. C. MUENSCHER. Pages 1–577; 123 figures. 1935. Published by the Macmillan Company, New York City. Price, $6.00.

Many books having a taxonomic background frighten one by the cold regimentation of the material. Here is a book that apparently lacks none of the language necessary for the proper identification of 500 common weeds and at the same time deftly carries the reader through pages of interesting material.

"Whether a plant of a given species is considered a weed depends not only on its characteristics and habits but also on its relative position with reference to other plants and man." Enlarging on this statement the author discusses the characteristics, habits of growth, methods of reproduction and dissemination of weeds.

In the prevention, eradication and control of weeds the discussion on chemical methods shows the enormous advances made during the last decade in the development of practical herbicides.

A key, glossary of terms, descriptions and control measures, beautiful full-page illustrations depicting more than 300 species, a list of important references to literature and an index containing common names and synonyms comprise the greater part of this latest unit of the Rural Science Series.—B. J. L.

INSECT ENEMIES OF SHADE-TREES, by GLENN W. HERRICK. Pages 1–417; 321 figures. 1935. Published by the Comstock Publishing Company, Inc., Ithaca, New York. Price, $5.00.

A discussion of insect enemies of shade-trees, certain shrubs and evergreens with practical recommendations for their control is presented in readable style with few technical terms.

If certain precautionary measures are exercised in the selection of trees, manner of planting, trimming and use of fertilizer the possibilities of insect damage are greatly reduced. The author gives a tentative arrangement of the more common shade-trees with regard to their susceptibility to insect attack.

The discussion of latest developments in gastrocides, contacticides, miscellaneous chemical and mechanical methods of insect control is followed by 24 chapters dealing with life-histories, nature of damage and best means of control of insects found on as many kinds of shade-trees. Other chapters deal with insect enemies of shrubs and evergreens other than pines. References to available literature appear throughout the text. In addition to an index to trees and shrubs a general index embracing a clear system of cross-referencing increases the utility of the book.

The fortunate combination of good paper, printing, original photographs and drawings increases the esthetic as well as practical value of this book.

—B. J. L.

AN APPARENT CORRELATION BETWEEN THE FEEDING HABITS OF CERTAIN PTEROMALIDS AND THE CONDITION OF THEIR OVARIAN FOLLICLES[1]

(Pteromalidae, Hymenoptera)

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During the past two years the Citrus Experiment Station, in cooperation with the Bureau of Entomology of the United States Department of Agriculture, has introduced into California from Europe several species of Hymenoptera parasitic on the alfalfa weevil, *Phytonomus variabilis*. Chamberlin (1924) lists eight important species. These are able to live under a rather large range of climatic conditions and most of them have at some time been introduced and colonized in the Rocky Mountain region of the United States. Only two species are known to be established, although the introduction work began twenty-three years ago.

In 1933 and 1934 colonies of the pteromalids, *Peridesmia*, *Spintherus*, *Eutelus*, and *Dibrachoides* were received at Berkeley, and liberations were made in the vicinity of Niles, California. This work was done under the direction of Professor Harry S. Smith of the Citrus Experiment Station.

Peridesmia phytonomi and *Spintherus* sp., which attack the weevil egg masses, were among the number previously introduced that failed to become established. Attempts to propagate them in the laboratory also had failed. In 1923 *Peridesmia* was recorded as destroying as high as 10 to 30 per cent of the egg masses in the vicinity of Hyéres, France, during the winter months of January and February. Since the winter climate of the West Coast is similar to that of the native habitat of the weevil parasites, further efforts to establish them seemed advisable.

An attempt was made again to breed them in the laboratory. They mated readily but they showed no interest whatever in

[1]Paper No. 309, University of California Citrus Experiment Station and Graduate School of Tropical Agriculture, Riverside, California.

the host material presented to them. The host material consisted of alfalfa stems containing egg masses of the weevil. Finally dissections were made to find out whether or not the parasites had any eggs to lay. Surprisingly, the ovaries in both *Peridesmia* and *Spintherus* were found to be completely devoid of either developing or mature eggs.

Some of the parasites had already been liberated, but more than a thousand were held in the laboratory at room temperature and fed on honey. At intervals for four months dissections were made for any ovarian change. The prospect seemed hopeless, so on October 28 about 600 females were liberated. All of the males meanwhile had died of senescence. About 125 parasites were retained for further observation. On January 28, 1934, only 10 of these were on hand, 1 *Peridesmia* and 9 *Spintherus*. An attempt was then made to reproduce them. When presented with host material, 3 of the *Spintherus* females became greatly interested. They located the punctures through which the weevil had deposited its eggs, although the aperture had been filled solid with excreta. The insertion of the ovipositor is stimulated by particles of excreta rather than by the presence of the host egg. Each female bored through the weevil puncture with its ovipositor and explored the egg cavity with it; but, instead of ovipositing, the ovipositor was thrust into one of the eggs. The parasite then execreted a viscous fluid which flowed down around the ovipositor and solidified. The ovipositor was then carefully withdrawn, leving a white waxlike tube through which the parasite sucked out the entire contents of the egg (Flanders, 1934).

Apparently the great need of the three parasites at that time was a protein diet, for a carbohydrate diet was available to them at all times. It is generally recognized that no reproduction is possible without the inclusion at some time of nitrogen in the diet. If an insufficient amount is stored up when in the larval stage, it must be obtained in the adult stage.

Genieys (1925) found that *Habrobracon brevicornis* fed on its host's body fluid prior to egg deposition as if it were necessary for the maturation of the eggs. Likewise H. D. Smith (1930) found that *Dibrachoides*, which attacks the pupa of the alfalfa weevil, never oviposits until it has imbibed the host's fluids. The fact that the males do not partake of this food also indicates that the need is correlated only with egg production. Ac-

cording to Smith, the host's fluids are the preferred food of the females. This preference, however, we find is exhibited only during oögenesis and maturation, and even then occasionally the desire for syrup or similar food may be dominant. When all of the oöcytes are in an early stage of development, the parasite prefers cane sugar syrup and shows no interest whatever in the host's fluids. This is apparently the case also with *Peridesmia*, *Spintherus*, and *Eutelus*.

The newly emerged adults of these weevil parasites possess ovarioles well filled with primary oögonia and oöcytes with their attendant nurse cells, but the nutritive chamber of each egg follicle is usually, if not always, larger than the oöcyte chamber.

The feeding of a parasite on the host's fluids apparently occurs when the oöcyte chamber in one or more of the follicles equals or exceeds the nutritive chamber. In the case of the weevil parasites the first host-feeding reaction occurs about six days prior to egg deposition. On the other hand, in another pteromalid, *Mormoniella*, which is parasitic on the pupa of flesh flies, egg deposition may occur prior to any host-feeding reaction. The oöcytes are in all stages of development when the parasite emerges from the host puparia. In this case the imago remains within the puparia until fully developed eggs are formed. Sufficient food is stored up during the larval period to permit the maturation of some of the eggs.

Six of the nine *Spintherus* females that were held over from the spring of 1933 never exhibted the host-feeding reaction although given every opportunity. The last of them died March 7, 1934. One of the three host-feeding females began egg-laying a week after the change in feeding habit occurred. She deposited 27 eggs in an 18-day period, which ended with her death. Although fresh egg masses were presented to her daily, she developed a need for carbohydrates after 12 eggs were laid. Then oviposition ceased for two days. Within two hours after the parasite had gorged herself with honey, oviposition commenced again. The occurrence of a similar need was noted with *Dibrachoides*. It appears, therefore, that the energy for continued oviposition was derived from the honey. Doten (1911) found that when *Pteromalus puparum* is supplied with fresh pupae, a female may lay eggs for three weeks; but if given honey also, will oviposit for two months.

Conditions in the laboratory appear to be for the most

part unfavorable for oviposition by *Spintherus*, since the other host-feeding females did not oviposit, although dissections a month later showed that a few oöcytes were present. *Peridesmia* proved to be even less adaptable to laboratory conditions.

Apparently the earlier portion of the spring brood of *Peridesmia* emerges with oöcytes in a more advanced condition than obtains in adults that appear later. In 1934, at the suggestion of Professor H. S. Smith, the Bureau of Entomology of the United States Department of Agriculture began the shipments several months earlier. About 250 females were reared from shipments received. These emerged over a period of 21 days. The parasites were isolated in vials and tested at three-day intervals for host-feeding reactions. This was accomplished by using alfalfa stems that had been placed for about 24 hours in containers with several weevils. The parasites that assumed the oviposition *posture* were in need of host fluids. The percentage of females in each daily emergence showing this reaction (within a period of one week of testing) decreased gradually from about 90 per cent to 25 per cent. The number of females in each daily emergence showing this reaction reached a peak six days before the peak of daily emergence. The reacting females probably represented the first brood of *Peridesmia* in the field and the non-reacting females of the second brood.

A few *Peridesmia* received from Europe in May and June, 1933, were submitted to this test but no reaction was noted.

One female *Peridesmia* that emerged prior to July 1, 1933, died February 21, 1934. During a period of at least 8 months, at temperatures between 60° and 80°F, it lived only on honey. A female that emerged March 28, 1934, and kept at temperatures between 65° and 85° F, died November 30, 1934. These parasites showed no interest when presented with host material. Eight months after emergence upon dissection the ovaries were found to be in a degenerate condition.

Only one egg has been deposited by *Peridesmia* under laboratory conditions. This was by a female which emerged March 13, from the 1934 shipments, commenced sucking host eggs March 17, and deposited an egg a week later. For three weeks it fed on the host eggs; then it ceased to do so and lost interest in its host material. A week later, 33 days after emergence, it was dissected and the ovaries were found to be

entirely empty of egg follicles. The ovarioles were greatly attenuated or lengthened, but the germaria at their tips were intact and not depleted. This observation indicated that the ovarian follicles had been absorbed. The single egg deposited and the continued feeding on the host for three weeks was evidence that oöcytes were present and were developing. The cessation of such feeding indicated that the protein need, which was due only to the presence of developing eggs, was again absent.

An examination of the ovaries of approximately 25 of the 250 females reared for liberation from the 1934 shipments confirmed this observation. The ovaries were stained in aceto-carmine and mounted on glass slides in Hoyer solution. Specimens were selected for dissection immediately after emergence from the alfalfa stem, immediately after beginning to feed on the host fluids, and soon after ceasing to feed on the host fluids. An attempt was made to stimulate egg development in females not exhibiting the host-feeding reaction by feeding them for a number of days on Royal Jelly and horse serum from pregnant mares, but no positive results were obtained.[2]

It appears then that if environmental conditions prevent oviposition, the ovarian follicles are absorbed, the feeding on host fluids ceases, and the parasite enters a long resting period during which it eats only carbohydrates.

The absence of follicles is characteristic of most of the females several weeks after their emergence whether they have exhibited the feeding reaction or not. Since the germarium seems to be always retained intact, staining densely with aceto-carmine, it seems probable that under certain conditions or after a certain elapsed time oögenesis will recommence.

The degeneration in the ovaries may be a form of what Wheeler (1910) called "phasic castration." This he defines as the inhibition of gonad development by seasonal or growth conditions. When in this state the adult parasites live for 8 or 9 months at room temperatures. In contrast to the long life of the adult is the short feeding period of the larva. *Spintherus* larvae feed for only one week and the others not much longer.

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[2]The author is indebted to Dr. Eckert, of the Agricultural Experiment Station, University of California, for furnishing a generous supply of Royal Jelly; and to Dr. Simpson, of the Institute of Experimental Biology, University of California, for the horse serum used.

Unlike many parasites, such as *Mormoniella*, they do not store up sufficient food during the larval stage to meet the requirements of egg production. It is interesting to note that these parasites destroyed more host eggs during the adult stage than when they were larvae.

Unlike *Spintherus* and *Peridesmia*, a portion of the 1933 shipment of *Dibrachoides* oviposited readily in the laboratory. About one-third of the material received from France in July oviposited. None of the offspring of these, however, nor of the remaining two-thirds of the original shipment contained developing eggs for several months after emergence.

Most of the *Dibrachoides* were liberated with the others on October 21, but a few were retained and on February 2, six were still alive. These were at least five months old, but none of them showed any interest in their hosts except one female which began ovipositing on February 6. She deposited 10 eggs during the following month. Upon dissection, 9 fully developed eggs were found in one ovary. The other ovary had apparently remained in a degenerate state. Nine females were reared from her eggs. Of these only the first and last deposited eggs. The others appeared to be in a condition of phasic castration.

Like *Dibrachoides*, it is possible that the first broods of *Peridesmia* and *Spintherus* contain two types of females, those capable of reproduction soon after emerging as adult imagos and those in which the maturation of the eggs is delayed for a considerable period. In the case of *Peridesmia*, however, the females of the first type if prevented from ovipositing appear to temporarily lose the ability to reproduce as a result of the degeneration of ovarian follicles and eggs. In the field the assumption of this condition would probably correspond with the low numerical status of the susceptible stage of the host. It is obvious that such parasites should be liberated within a week from emergence or held in the laboratory until the following season.

The type of ovarian development in weevil parasites may be due to a correlation with the ovarian development of their host. This is supported by the fact that Snow (1928) found that the eggs of the weevil did not mature until four months after it reached the adult stage. Like their host, *Peridesmia*, *Spintherus*, and *Dibrachoides* aestivate in the field as adults. Some, if not all, of the progeny of the aestivating broods

normally oviposit soon after emergence. If host material is not available, they may undergo phasic castration. When the second-generation adults emerge, they appear to be in a condition of phasic castration. This condition characterizes the aestivating broods of both host and parasite.

SUMMARY

Observations of certain parasitic Hymenoptera, particularly the pteromalids *Dibrachoides*, *Peridesmia*, *Spintherus*, and *Eutelus*, show that when the ovarian follicles reach a certain stage of development a change occurs in the food habits of the female. In the laboratory this change was from a diet of only cane sugar syrup or of honey to a protein diet consisting of the body fluids of the host species. After the beginning of the period of egg deposition, a certain amount of carbohydrates appears to be needed in addition to the host's fluids.

When environmental conditions inhibit oviposition, the ovarian follicles and the eggs apparently disintegrate and are absorbed and the parasite reverts to a purely carbohydrate diet. (In *Peridesmia* this may occur within three weeks after the first change in diet.) This absorption of the contents of the ovaries (except the primary cells in the germarium) may also occur in females that did not develop a need for the host's fluids.

A period of "phasic castration" follows, which may last as long as nine months at temperatures between 65° and 80° F. The end of this period is apparently synchronized with the appearance in the field of the susceptible stage of the host.

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DYAR'S RULE AS RELATED TO THE NUMBER OF INSTARS OF THE CORN EAR WORM, HELIOTHIS OBSOLETA (FAB.), COLLECTED IN THE FIELD

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The original purpose of the investigation described in this paper was to find out whether the number of instars of the corn ear worm varies under field conditions and, if so, to what conditions of food or environment the variation can be attributed. This project was conceived and the work done entirely by the senior author.

In careful investigations on number of instars reference is usually made to the work of Dyar (1890). This was done by the senior author in his original manuscript, which was reviewed by the junior author. The latter, having made a number of comments on the significance of Dyar's work, was invited to discuss and interpret it in the present manuscript in connection with the data on the corn ear worm.

BACKGROUND OF METHOD

Two important generalizations may be traced to Dyar (1890). In the light of present knowledge they may be stated in expanded form as follows: (1) The sclerotized parts of insects do not change in area during a stadium, the increase in areas of these parts during larval development occurring only at ecdysis. (2) The discontinuous or steplike increase in the dimensions of the sclerotized parts of insects during larval development usually takes the form of a geometrical progression.

Only the second generalization should be called Dyar's law or Dyar's rule. It will be discussed in another section of this paper. For the present, attention will be confined to the first generalization, which is the basis of the present method for determining the number of instars of the corn ear worm.

From the first generalization it follows that any instar of a species can be characterized by a dimension of a sclerotized part of the body of any individual of that instar, provided the range of variation of

[1] In cooperation with the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture.

the dimension among individuals of the instar does not overlap that of the next preceding or succeeding instar. Dyar did not study the range of variation of the width of the head capsule among individuals of an instar, but nevertheless recommended the characterization of instars of lepidopterous larvae by this dimension. Dyar himself and many other entomologists who followed his recommendation thereafter included head measurements in their descriptions of the instars of insects. Evidence to support the soundness of Dyar's recommendation began to accumulate many years later when adequate samples were measured in each instar and it was shown that the ranges of variation of the chosen dimension in the several instars usually do not overlap.

Quaintance and Brues (1905) may have been the first to publish measurements of more than 100 specimens. They gave the range of variation of the width of cast head capsules of *Heliothis obsoleta* (Fab.) in each of six instars. There was no overlapping. As their larvae were reared and the molts were observed, they evidently knew the number of instars of their material before the measurements were made. However, their results show that the number of instars could have been determined from the same material without a knowledge of the number of molts. If, after measuring all the head capsules, they had arranged the measurements in numerical order, they would have observed 5 gaps in an otherwise continuous series of increasing head widths. In other words, they would have found 6 separate groups of measurements, each representing an instar.

A study of the literature does not indicate who first grasped the possibility of determining the number of instars by the grouping of measurements. Dyar himself may not have pointed it out because the nature of his work did not require its application. It is evidently suited particularly for the determination of the number of instars of larvae the molts of which cannot be readily observed; e. g., larvae living within plants, animals, soil, or stored products. Peterson and Haeussler (1928) were probably the first to put the method to a thorough text for this purpose. Working with the oriental fruit moth, *Grapholitha molesta* (Busck), they reasoned that if samples of larvae are removed from fruit at intervals during the development of a brood, each sample should contain representatives of one or more instars; and, if the samples are taken frequently enough, each instar should be well represented in the whole collection. Then, if the heads of all collected larvae are measured, the measurements should fall into more or less discontinuous groups, each group representing one instar. The measurements when represented graphically as column diagrams should form a series of separate distributions each representing the variation in width of the head capsule among the individuals of an instar. Even if these distributions should overlap somewhat, the number of instars could still be determined if the distributions were distinctly unimodal, the number of instars being equal to the number of peaks in the diagram.

By the method of Peterson and Haeussler (1928) the number of instars of six species of inaccessible larvae has been studied recently by Taylor (1931), Metcalfe (1932), Andrewartha (1933), Prebble

(1933), McDougall (1934), and Fife.[2] This method has not always been successful; and some of the limitations of it can be pointed out from examples in the literature. Metcalfe (1932) failed to determine the number of instars of *Sitodrepa panicea* (L.) because the measurements did not fall into discontinuous groups and so many irregular peaks appeared in the frequency distributions that their meaning was obscure. Metcalfe suggested that the rate of development of the sexes may have differed sufficiently to yield two series of curves which merged into each other. It is obvious that the method of Peterson and Haeussler will give clear results only when the insects being measured are fairly homogeneous in rate of development and number

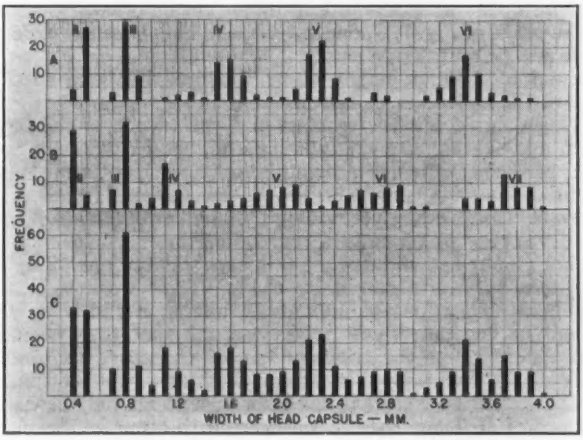

FIG. 1. Frequency distributions of head measurements of the black cutworm from data of Satterthwait. A = larvae having 6 instars, B = larvae having 7 instars, C = A and B combined.

of instars. If the population being studied is a mixture of individuals having n and $n+1$ instars and a corresponding difference in rate of development, it might be difficult or impossible to interpret the frequency distributions.

As an illustration of what would happen in this case, the measurements of Satterthwait[3] (1933) on the black cutworm, *Agrotis ypsilon* (Rott.), having 6 and 7 instars in both sexes, are represented graphically, separately for each number of instars (Fig. 1, *A* and *B*) and together for the whole population, (Fig. 1, *C*). The first instar, which was quite distinct from the second in both 6 and 7 instar larvae, was omitted from the diagrams because only a relatively small number of individuals

[2]Manuscript on pink bollworm being prepared for publication.

[3]The writers are indebted to A. F. Satterthwait, Division of Cereal and Forage Insects, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, for supplying the individual measurements.

was measured. The measurements were made to 0.01 mm. but in the diagrams they are classified to 0.1 mm; that is, measurements between 0.35 and 0.44 mm., inclusive, are called 0.4 mm., and so on. Only measurements of larvae that became adults were used in the diagrams.

Figure 1, *A* and *B*, shows that the number of instars of either the 6 or 7 instar larvae could have been determined from the frequency distributions alone, for the several groups of measurements stand out distinctly, usually with a definite peak in each group. If, however, the 6 and 7 instar larvae had been mixed, as they might be in collections made at random, the measurements would appear as shown in Fig. 1, *C*. Here there is no longer a distinct separation between groups of measurements, the peaks of the 6-instar larvae filling the valleys of the 7-instar larvae in the intermediate portion of their development. From the peaks of Fig. 1, *C*, one might guess that 8 instars were present, which would be quite erroneous.

The same situation might occur if more than one species were present in the collection of larvae.

Having pointed out the relation of Dyar's work to the method of Peterson and Haeussler and its limitations, the writers pass on to the present investigation. Hitherto this method has been applied to determining the number of instars of inaccesible larvae. It would seem equally suitable for determining the number of instars of accessible larvae developing under natural conditions in the field. Quaintance and Brues (1905) had shown that 6 instars was the prevailing number for the corn ear worm reared by them. Their work indicated that nearly equal proportions of individuals having n and $n + 1$ instars would not be encountered in collections and that there would be no marked difference in the development of the sexes to obscure the meaning of the frequency-distribution diagrams. As for the identity of the species[4] to be collected, no other species having the habits and appearance of *Heliothis obsoleta* was known to occur in the plants and region where the collections were to be made.

PROCEDURE AND RESULTS

Larvae representing four broods of the corn ear worm were collected from crops growing in the Brazos River bottom about 10 miles from College Station, Tex. From 40 to 50 larvae were collected every two or three days, beginning when the first instar appeared and continuing until the largest worms were abundant. The first brood was taken from the stalks of corn during the latter part of April and in May; the second, from corn ears during June; the third, from corn ears and cotton during July; and the fourth, from hegari during August. These were the crops most susceptible to attack by the broods collected from them.

The larvae were preserved in Kahle's fluid. The width of head capsules was measured later by ocular micrometer to the nearest

[4]Carl Heinrich, Division of Insect Identification, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, very kindly examined 1,450 specimens that had been measured. With the exception of one specimen of *Heliothis virescens* (Fab.), all were found to be *Heliothis obsoleta*.

division. A table was prepared to cover all measurements ranging from 6 to 84 divisions in steps of 1 division, or, expressed in millimeters, from 0.2526 mm. to 3.5364 mm. in steps of 0.0421 mm. The numbers of larvae the measurements of which fell in each of the 79 steps were recorded. Since the measurements were distributed in distinct groups, the number of instars of each brood was clearly indicated. From this table of raw data Table I (p. 450) was calculated, giving the mean width of the head capsule of the individuals in each instar and the probable error of the mean, the coefficient of variation, and the ratio between the mean head width of each instar and that of the one next preceding. This ratio is sometimes known as the growth ratio or Dyar's ratio.[5]

Also from the table of raw data Fig. 2 was drawn to show graphically the frequency distribution of the measurements. As the columns form

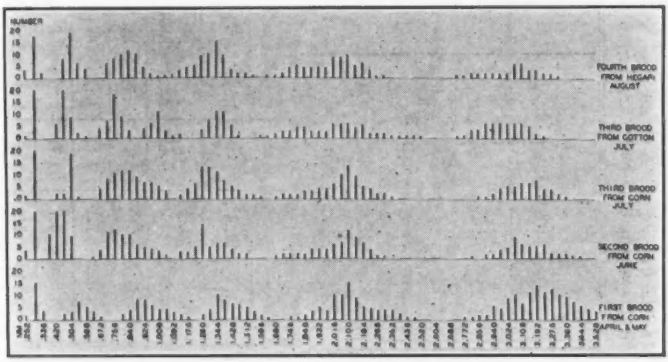
NUMBER
FOURTH BROOD FROM HEGARI AUGUST
THIRD BROOD FROM COTTON JULY
THIRD BROOD FROM CORN JULY
SECOND BROOD FROM CORN JUNE
FIRST BROOD FROM CORN APRIL & MAY

FIG. 2. Frequency distributions of head measurements of the corn ear worm.

distinct unimodal groups that do not overlap, each group clearly represents one instar. In the broods collected from corn and hegari there were six groups or instars, and in the brood from cotton there were seven groups or instars.

The development of the broods of the corn ear worm on the several hosts is shown in Fig. 3. The numbers of the instars are equally spaced on the arithmetic scale of semilogarithmic cross-section paper and the head measurements are plotted on the logarithmic scale. This method of illustrating the rate of development of the head per instar was published recently by Forbes (1934). As he pointed out, it has the advantage of giving a straight line when the progression is perfectly geometrical. Deviations from a straight line indicate departures from a geometrical progression.

[5]In all his work Dyar calculated this ratio by dividing the head width of an instar by that of the succeeding instar. The reciprocal of this ratio has lately found wide acceptance and is used in the present paper, because it indicates growth directly, i. e., the greater the ratio the greater the growth.

TABLE I

MEAN HEAD WIDTHS OF LARVAE OF *Heliothis obsoleta*, COEFFICIENT OF VARIATION, AND THE RATIO BETWEEN THE MEAN OF EACH INSTAR AND THE ONE NEXT PRECEDING

BROOD AND HOST	FIRST INSTAR		II/I	SECOND INSTAR		III/II	THIRD INSTAR		IV/III
	Mean (I)	C. V.		Mean (II)	C. V.		Mean (III)	C. V.	
	Mm.	*Percent*		*Mm.*	*Percent*		*Mm.*	*Percent*	
First, from corn	0.297±0.003	7.0	1.90	0.563±0.008	10.4	1.70	0.958±0.009	9.8	1.48
Second, from corn ears	0.291±0.001	4.0	1.51	0.439±0.003	8.6	1.86	0.818±0.008	12.2	1.60
Third, from corn ears	0.293±0.001	2.4	1.69	0.496±0.004	5.5	1.70	0.844±0.008	11.9	1.57
Third, from cotton	0.293±0.004	9.7	1.61	0.473±0.004	7.0	1.61	0.760±0.004	5.5	1.32
Fourth, from hegari	0.293±0.001	3.0	1.74	0.510±0.004	6.9	1.63	0.829±0.007	8.6	1.58

BROOD AND HOST	FOURTH INSTAR		V/IV	FIFTH INSTAR		VI/V	SIXTH INSTAR		VII/VI	SEVENTH INSTAR	
	Mean (IV)	C. V.		Mean (V)	C. V.		Mean (VI)	C. V.		Mean (VII)	C. V.
	Mm.	*Percent*		*Mm.*	*Percent*		*Mm.*	*Percent*		*Mm.*	*Percent*
First, from corn	1.422±0.009	6.4	1.48	2.108±0.011	6.9	1.52	3.211±0.010	5.2			
Second, from corn ears	1.308±0.012	9.7	1.56	2.043±0.012	7.0	1.54	3.140±0.013	4.3			
Third, from corn ears	1.327±0.008	7.3	1.55	2.055±0.012	7.1	1.52	3.125±0.011	3.6			
Third, from cotton	1.006±0.007	5.5	1.35	1.359±0.006	3.7	1.49	2.026±0.017	10.4	1.48	3.007±0.011	3.9
Fourth, from hegari	1.310±0.008	7.9	1.53	2.005±0.013	7.8	1.53	3.060±0.016	4.8			

Figure 3 shows that the development of three broods of the corn ear worm on corn and one on hegari was much the same. Development on cotton was similar to that on corn and hegari near the beginning and end of the larval stage, but between the second and fifth instars a retardation occurred that led to an additional instar, the fourth in this case. Dyar (1895b) would have called this fourth instar an "interpolated stage" (P in Fig. 3). The development was not perfectly geometrical in any of the five cases.

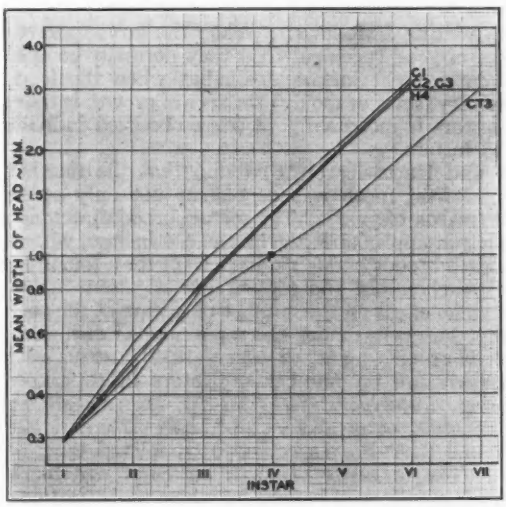

FIG. 3. Relation between instars and head measurements of the corn ear worm to show particularly the difference in development of the third brood from cotton and the broods from corn and hegari. C1, C2, and C3 = first, second, and third broods from corn, respectively. CT3 = third brood from cotton. H4 = fourth brood from hegari. *P* indicates "interpolated instar."

EFFECT OF FOOD AND TEMPERATURE ON NUMBER OF INSTARS

The literature shows that the number of instars is variable in many species of insects and depends largely on the nutritive value of the food, which of course may be affected by environmental factors. Dyar (1895a) recognized the influence of food. He wrote as follows on *Clisiocampa fragilis* Stretch: "Most of the larvae had but five stages, but a few less vigorous ones had six stages . . . It is . . . a matter of degree of nutrition whether they complete their growth in five stages or in six . . ." Quaintance and Brues (1905) wrote of the corn ear worm (cotton bollworm) as follows: "Of 100 larvae reared in the laboratory at Paris, Tex., in 1904, 90 percent molted 5 times, 8 percent 4 times, and 2 percent 6 and 7 times, respectively . . . Highly nutritious food and excessive care in breeding apparently caused less

than the normal number of molts. Seven out of eight larvae reared on cowpeas molted thus. Molts in excess of the normal were caused by neglect and insufficient or disagreeable food." The senior author found 6 instars to be the prevailing or normal number, as did Quaintance and Brues. He believes that the brood from cotton had seven instars because this plant was less succulent than corn or hegari. Of course the phrase "less succulent" is vague and unsatisfactory, but is the best description of difference among these crops that can be given in the absence of chemical analyses. Decker (1931) drew the same inference from his observations of the stalk borer, *Papaipema nebris nitela* Guen., writing as follows: "When the larvae are supplied with an abundance of good succulent food they normally complete development in seven or eight instars . . . but when the food is of poor quality (hard, dry, sour, or moldy) the rate of growth is reduced and the number of instars is increased." Decker observed individuals having from 9 to 15 instars.

Peterson and Haeussler (1928) found that the number of instars of the oriental fruit moth was dependent not only on food but on temperature (season of year). The second brood, hatching on June 26 and developing in apples and peaches, had 4 instars, whereas the first, third, and fourth broods had 5 instars, except for a fourth brood having 4 instars in peaches. In the present investigations temperature appeared to have no effect on the number of instars of the corn ear worm, the spring brood on corn having the same number of instars as the two summer broods on this plant. Decker (1930) also failed to find any effect of temperature on number of instars in experiments on the four-lined borer, *Luperina stipata* (Morr.). Nearly all larvae reared on young succulent cornstalks at 13°, 23°, 27°, and 33° C. (55.4°, 73.4°, 80.6°, and 91.4° F., respectively) completed their development in 7 instars. The influence of food, however, was marked, woody cornstalks producing larvae having as many as 11 instars.

THE USE OF DYAR'S RULE FOR CORROBORATING THE NUMBER OF INSTARS OBSERVED[6]

Dyar (1890) stated that "The widths of the head of a larva in its successive stages follow a regular geometrical progression." This statement became known as Dyar's rule or Dyar's law. If it is generally true, it follows, as Dyar pointed out, that observed progressions showing lack of regularity must be regarded with suspicion, indicating perhaps that a molt has been overlooked.

Outside of Dyar's own work, the writers have not been able to find a case in the literature in which the application of Dyar's rule led to the discovery of an instar that had been overlooked. Nevertheless the rule is still used for corroborating the number of instars observed, and a few years ago Taylor (1931) guardedly recommended it for this purpose. It has been the practice to use the mean of the observed growth ratios as a common ratio for calculating a progression beginning

[6]For mathematical assistance on this section the writers are indebted to G. R. Elwell, Bureau of Lighthouses, U. S. Department of Commerce, and C. M. Purves, Bureau of Agricultural Economics, U. S. Department of Agriculture.

with the first or last term of the observed progression. Having recorded the observed and calculated values side by side, the entomologist usually decides by guess that the agreement is reasonably close and hopes that his observations on the number of instars have been confirmed. It is the purpose of this section to analyze certain observed and calculated progressions in order to judge the reliability of Dyar's law for corroborating the number of instars.

Table II, *A*, (p. 454), shows observed and calculated values for the first brood of the corn ear worm as presented by the senior author in his original manuscript. The calculated progression was derived from the mean growth ratio and the first term of the observed progression. All the differences between observed and calculated values have the same sign, showing that the deviations are unbalanced and indicating that some other growth ratio and first term should give a progression in better agreement with the observed progression.

The first problem is to find the values of a growth ratio and first term that will yield a geometrical progression in best possible agreement with the observed progression. It has already been pointed out that a perfect geometrical progression of head widths can be represented by a straight line, if the logarithms of the head measurements are plotted against the numbers of the instars. The equation of this line is $\log y = a + bx$, where y is the width of the head capsule, x is the number of the instar, and b is the slope of the line or the logarithm of the desired growth ratio. By the method of least squares values for a and b were found that gave an equation for the straight line best fitting the observed head measurements. This equation is $\log y = -0.67476 + 0.20174\,x$, from which the growth ratio is 1.591 and the first term 0.336. The remaining five terms of the calculated progression can be computed from this growth ratio and first term, or all can be found by substituting for x in the foregoing equation. These calculated values are given in Table II, *B*, together with the differences between them and the observed values. The signs of the differences are now equally divided and the algebraic sum of the differences approaches zero. The algebraic sum of the differences of the logarithms of the observed and calculated values is zero and the sum of their squares is a minimum. The observed values are plotted in Fig. 4, and the line of best fit is shown as a solid line. A dotted line is also shown representing the progression calculated by the use of the mean of the observed ratios and the observed first term (method A). It is obvious that method A, which has been generally used, fails to give a line that fits the points in this case. The dot-and-dash curve in Fig. 4 will be discussed later.

Having calculated a geometrical progression that is in the best possible agreement with the observed measurements, we are now in a position to inquire whether this progression corroborates the number of instars observed for the first brood of the corn ear worm. Let it be assumed that the second instar was overlooked and that there were 7 instars instead of 6. For the purpose of calculation the observed second instar becomes the assumed third, and the observed third becomes the fourth, and so on. The method of least squares was applied again and the progression so calculated is compared with the assumed pro-

TABLE II

COMPARISON OF OBSERVED AND CALCULATED VALUES (IN MILLIMETERS) OF THE MEAN WIDTH OF THE HEAD CAPSULE OF THE FIRST BROOD OF THE CORN EAR WORM

	Method of Calculation[7]	INSTAR						
		I	II	III	IV	V	VI	VII
Observed	A	0.297	0.563	0.958	1.422	2.108	3.211	
Calculated r = 1.6026		0.297	0.476	0.763	1.223	1.960	3.141	
Difference		0.000	+0.087	+0.195	+0.199	+0.148	+0.070	
Difference (percent)		0.000	+18.3	+25.5	+16.3	+7.5	+2.2	
Observed	B	0.297	0.563	0.958	1.422	2.108	3.211	
Calculated r = 1.591		0.336	0.535	0.852	1.356	2.158	3.434	
Difference		—0.039	+0.028	+0.106	+0.066	—0.050	—0.223	
Difference (percent)		—11.6	+5.2	+12.4	+4.9	—2.3	—6.5	
Observed	C	0.297		0.563	0.958	1.422	2.108	3.211
Calculated r = 1.497		0.280	0.419	0.628	0.940	1.407	2.106	3.152
Difference		+0.017		—0.065	+0.018	+0.015	+0.002	+0.059
Difference (percent)		+6.0		—10.4	+1.9	+1.0	+0.1	+1.8
Observed	D	0.297	0.563	0.958	1.422	2.108	3.211	
Calculated		0.305	0.546	0.922	1.466	2.200	3.113	
Difference		—0.008	+0.017	+0.036	—0.044	—0.092	+0.098	
Difference (percent)		—2.6	+3.1	+3.9	—3.0	—4.2	+3.1	

[7]The four methods of calculation indicated by letters in this column are as follows:

A, Calculated from the mean of the observed ratios (see Table I) and the observed first term.

B, Calculated by the method of least squares, using the equation $\log y = a + bx$.

C, Calculated like B, but assuming seven instars with the second missing.

D, Calculated like B, but using the second-degree equation $\log y = a + bx + cx^2$.

gression in Table II, C. This calculated progression agrees with the assumed progression better than either of the two previously calculated (A and B) agrees with the observed progression. The better fit obtained by assuming the existence of 7 instars is shown more clearly in Fig. 5, in which the solid line is the same as in Fig. 4 and the dotted line represents the progression calculated for 7 instars. It has therefore been shown that the application of Dyar's rule by the method of least squares does not corroborate the number of instars observed in this case. Instead, it indicates that the second instar was overlooked.

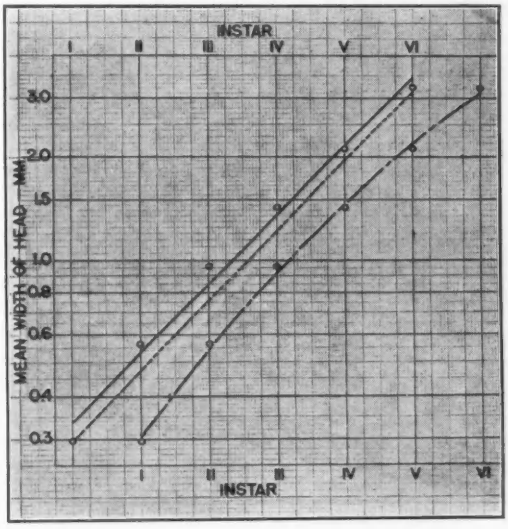

FIG. 4. Relation of calculated progressions to observed head measurements of the first brood of the corn ear worm. The circles represent the observed mean head widths for each instar. The solid line is a straight line of best fit calculated from the equation $\log y = a + bx$. The dotted line is a straight line of poor fit calculated from the average growth ratio and the observed first term. The dot-and-dash line is a curve of best fit calculated from the equation $\log y = a + bx + cx^2$. The upper instar scale refers to the lines, the lower instar scale to the curve.

Nevertheless, the writers are convinced for the following reasons that the second instar was not overlooked:

Figure 2 shows no large gap between the first and second groups of measurements into which a hypothetical second instar might fit. Moreover, there is no reason for supposing that another instar should fit into the existing small gap, if it can be shown that this observed progression is not unusual. The trend of a progression of head measurements can be judged by the growth ratios between instars. If the progression is perfectly geometrical, all ratios are the same. If not,

deviation from a geometrical progression is indicated. The observed ratios for the first brood of the corn ear worm (Table I) tend to become smaller from the first to the last instar. The same tendency, though less marked, is noted in three other series in Table I. The II/I ratio, 1.90 is the largest in Table I. Have ratios as large as this been found by others in lepidopterous larvae and does the literature show that the ratios tend to diminish during development?

The junior author has searched the literature thoroughly and has found 45 pairs of head measurements of lepidopterous larvae, most of

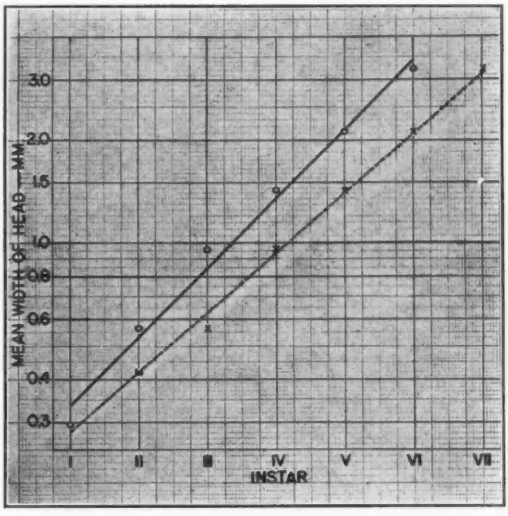

FIG. 5. Relation of calculated progressions to head measurements of the first brood of the corn ear worm. The circles represent the observed mean head widths for each observed instar; the crosses represent observed mean head widths for each assumed instar. The solid line is the same as in Fig. 4. The dotted line was calculated in the same way, but under the assumption that 7 instars existed and that the second (*M*) was overlooked. A line of better fit was thereby obtained.

them by Dyar, that yield growth ratios equal to or greater than 1.90. Such a high ratio standing alone in a series of lower ratios might be considered to indicate an overlooked instar, but Dyar himself did not so interpret it. Dyar (1892) noted a II/I ratio of 1.97 in *Nadata oregonensis* Butler, the other ratios ranging from 1.25 to 1.47. He explained this ratio, not by assuming that he had overlooked the second instar, as his own rule would indicate, but by supposing that "normal stage II does not occur."

The largest ratios in Table I occur in the early instars. In looking through the literature it seemed to the junior author that cases of diminishing ratios were usual rather than unusual. In order to verify

this impression, 820 ratios[8] for lepidopterous larvae were divided into two groups, 401 for the first half of larval development and 419 for the last. The mean ratio for the first group was 1.56 and for the second 1.46, showing definitely the tendency of growth ratios to diminish during development. Data on other orders of insects seem to show the same tendency. This trend has been noted by others. From a study of the development of noctuid larvae Ripley (1923) concluded that "the increase from first to second stadia is usually greater, from penultimate to last more often less than for other molts." He was struck by "the inconstancy of Dyar's supposed constant . . . ranging in *Agrotis ypsilon*, for instance, from 1.28 to 1.84." In his study of the data of Satterthwait (1933) Forbes (1934) noted a falling off in the ratios for *Agrotis ypsilon* toward the end of its development.

From the two preceding paragraphs the writers conclude that the observed development of the first brood of the corn ear worm was not unusual, and that there is no good reason to suppose that the second instar was overlooked, as the application of Dyar's rule would indicate. Dyar's rule is merely an approximation that can not be expected to hold in every case. Examples of almost perfect agreement with the rule can be found in the literature, and, on the other hand, examples of deviations can be found which are so great, as in the present case, that the rule can not be relied upon for the corroboration of the number of instars observed. As Forbes (1934) pointed out, "There is still much room for study of the exceptions and irregularities in this law."

What conclusions would be reached by applying Dyar's rule to the other four series of data on the corn ear worm given in Table I? To answer this question the same sort of calculations were made that were described above and summarized for the first brood in Table II. It will not be necessary, however, to present the results of the calculations on the last four series in the same detail. All that is needed for purposes of discussion is a measure of the goodness of fit of each calculated progression to the observed head measurements. Such a measure is afforded by the standard error of estimate, which is simply the standard deviation of the observed measurements from the calculated measurements. The standard error of estimate was calculated exactly as described by Mills (1925, p. 292) for a similar problem, using percentage differences, as are given in Table II. However, instead of dividing the sum of the squares of the percentage deviations by n they were divided by $n - 2$ for the straight lines and $n - 3$ for the curves, an adjustment recommended by Ezekiel (1930, p. 121). The results are given in Table III. For the moment let us consider only the standard errors of estimate for four methods of calculation on the data for the first brood. Note that each successive method of calculation gives a lower standard error, or, in other words, a better agreement between observed and calculated values. The fourth method (D) was applied because the trend of the growth ratios indicated that the observations would be fitted better by a curve than by a straight line. A curve of best fit was calculated from the equation

[8]The data on which these calculations are based were taken from 155 papers, 113 of them by Dyar. It is obviously impracticable to cite them.

$\log y = a + bx + cx^2$ by the method of least squares. As expected, method D gave the best agreement of the four between observed and calculated values. The detailed results by method D for the first brood of the corn ear worm are recorded in Table II, *D*, and are shown graphically in Fig. 4, dot-and-dash curve.

Table III shows that in all cases method A, the one previously used by entomologists, gives the poorest fit and method D the best fit. Only methods B and C are involved in deciding whether or not Dyar's rule verifies the number of instars observed. If the error obtained by assuming an additional instar is greater than that based

TABLE III

STANDARD ERRORS OF ESTIMATE OF PERCENTAGE DIFFERENCES BETWEEN OBSERVED AND CALCULATED MEAN HEAD WIDTHS OF THE CORN EAR WORM

BROOD AND HOST	METHOD OF CALCULATION[9]			
	A	B	C	D
First, from corn	*Percent* 18.1	*Percent* 9.8	*Percent* 6.2[10]	*Percent* 4.8
Second, from corn ears	7.5	5.6	7.0[11]	5.4
Third, from corn ears	10.5	5.1	8.9[11]	1.2
Third, from cotton	9.6	7.2		6.8
Fourth, from hegari	8.9	4.9	10.5[11]	1.4

[9]The letters indicating the methods of calculations have the same meaning as in Table II (q. v.).

[10]It was assumed that the second instar was overlooked.

[11]It was assumed that the third instar was overlooked.

on the observed number of instars, it may be said that the number of instars observed has been confirmed by the application of Dyar's rule, as in the case of the second and third broods from corn and the fourth brood from hegari. If the reverse is true, as in the first brood from corn, it must be concluded that Dyar's rule has not corroborated the number of instars observed, but, as already explained, it does not necessarily follow that an instar has been overlooked.

Two examples from the literature will now be given for additional evidence showing that the application of Dyar's rule occasionally fails to verify the number of instars observed, although there may be every other reason to believe that no instar was overlooked.

In Fig. 6, which is similar in construction to Fig. 5, are shown the lines of best fit for the data of Peterson and Haeussler (1928) on the width of head capsule of their series H of the oriental fruit moth in peach, in which 5 instars were found. The dotted line for 6 instars with the second missing fits the data distinctly better than the solid line for the observed 5 instars. However, the frequency distribution

of these measurements illustrated by Peterson and Haeussler shows that not more than 5 instars were present and that their series H probably consisted of a mixture of 4 and 5 instar larvae, giving a somewhat obscure distribution, as pointed out by the present writers in Fig. 1.

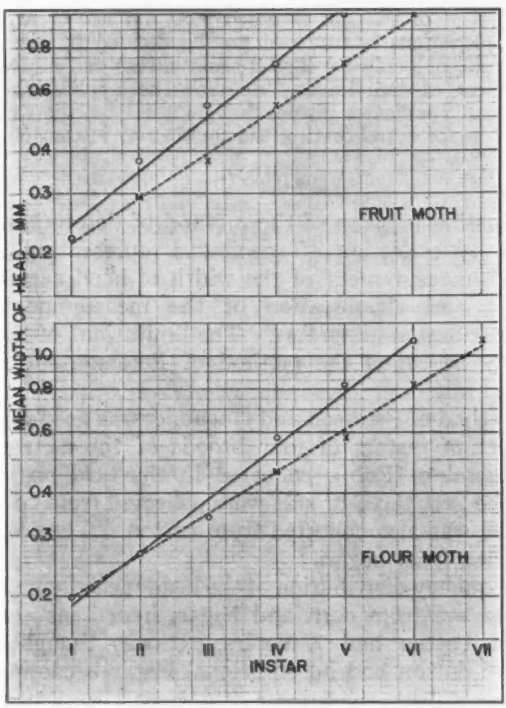

FIG. 6. Relation between instars and head measurements of the oriental fruit moth (Peterson and Haeussler, series H) and the Mediterranean flour moth (Brindley) to show closer approach of the measurements to a geometrical progression (straight line) when it is assumed that an instar has been overlooked. Solid lines for n observed instars; dotted lines for $n + 1$ instars. X represents points that were moved one instar space to the right. M indicates a hypothetical missing instar. This figure is similar to Fig. 5.

Also in Fig. 6 are shown the lines of best fit for the data of Brindley (1930), who observed 6 instars in the Mediterranean flour moth, *Ephestia kuehniella* Zell. The dotted line for 7 instars with the fourth missing fits the data much better than the solid line for the observed 6 instars. However, this species was reared under constant conditions of temperature and relative humidity and individuals were observed daily. Measurements were made of 100 larvae. Therefore, it cannot

be doubted that there were only 6 instars under the conditions in which the larvae were reared.

The whole argument can be reduced to very simple terms. When one relatively high growth ratio occurs in a series, as in the writers' data on the first brood of the corn ear worm or in Brindley's data on the Mediterranean flour moth, it indicates either that an instar has been overlooked or that an expected molt did not occur. Which of the two explanations is true can not be decided by the application of Dyar's rule, but only by careful observations and measurements of large numbers of individuals. Because the application of Dyar's rule occasionally indicates instars that do not exist, the writers do not recommend it for corroborating the number of instars observed.

SUMMARY

A discussion is given of the method of determining number of instars by collection of specimens representing all instars of a brood, measurement of the width of head capsules of the individuals, and classification of the measurements in frequency-distribution diagrams. The limitations of the method, which may be called the method of Peterson and Haeussler, are pointed out.

The method of Peterson and Haeussler was used to determine the number of instars of four broods of the corn ear worm, *Heliothis obsoleta* (Fab.), collected in the field on susceptible crops. The first three broods were collected from corn and the third brood was also collected from cotton. The fourth brood was obtained from hegari.

The frequency distribution of the head measurements showed that the larvae from corn and hegari had 6 instars, whereas those from cotton had 7 instars. It was thought that the larvae from cotton had an additional instar because this plant was less succulent than corn and hegari and consequently was less suitable for the development of the larvae. Seasonal temperatures appeared to have no effect on the number of instars, for the spring brood from corn had the same number of instars as the two summer broods from this plant.

The application of Dyar's rule for corroborating the number of instars observed in the corn ear worm was studied mathematically. Four methods were used to calculate progressions for comparison with the observed progressions of mean head widths. The calculated geometrical progressions were shown as straight lines on semilogarithmic cross-section paper.

By the method of least squares and by calculation of the standard errors of estimate it was shown that the mean head

widths of the first brood of the corn ear worm fitted a geometrical progression of 7 terms much better than one of 6 terms, the observed number. It was necessary to conclude either that the second instar of 7 was overlooked, or that Dyar's rule was not valid for this particular case. It was concluded that Dyar's rule did not hold, because the progression in question was not unusual, as shown by a study of the literature. High growth ratios are often encountered in the early part of larval development, and there is a tendency for growth ratios to diminish during larval development. Two examples from the literature are given as additional evidence that the application of Dyar's rule may indicate instars that do not exist. Therefore, the writers do not recommend the use of Dyar's rule for corroborating the number of instars observed.

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NOTES ON SOME HOLOLEPTINAE FROM SOUTH AMERICA

(Histeridae, Coleoptera)

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Reading, Pa.

Dr. S. H. Williams, of the University of Pittsburgh, has had the kindness to give me for study the Histerid beetles from his collection of Coleoptera made on several trips to Kartabo, British Guiana. The Hololeptines represented, while few in number, are of great interest, two new species representing a new genus being among them. The writer has also included in this paper, notes made on the collection of the group at the Carnegie Museum.

The following key is in great part a translation from Bickhart (Genera Insectorum, fasc. 165; 1916) but includes the several new genera erected since the date of that publication.

KEY TO THE GENERA

1. Mandibles more or less equal in both sexes; frontal margin forms a protruding tooth before the eyes 2
   Left mandible in male much heavier and somewhat longer than the right; margin rounded before the eyes ..... **Oxysternus**
2. Labrum fairly large, in front deeply incised, the two lobes thus formed are about as long as broad at the base 3
   Labrum very short, the lobes small, tubercleform 7
3. Mesosternum emarginate before; tibiae, at least hind ones, dentate 4
   Mesosternum truncate; tibiae toothless on outer edge ..... **Dimalus**
4. Body above strongly flattened 5
   Body above strongly convex; prosternum narrowed rather strongly anteriorly; mandibles strong, toothed ..... **Eutidium**
5. Mandibles swollen internally but not toothed, elongate; mentum distinctly transverse, deeply incised ..... **Petalosoma**
   Mandibles toothed internally, smaller, robust; mentum more or less quadrate, truncate or arcuately rounded before 6
6. All tibiae distinctly dentate; mentum small, arcuate before, truncate behind, quadrate ..... **Phylloma**
   Protibiae with three or four tubercles externally; mentum large, slightly transverse, truncate and bilobed before, with a tooth behind each mandible ..... **Platyeutidium**
7. The middle and hind tibiae with all three teeth coming off separate processes, subequally spaced; prosternum carinate, terminating in a sharp spine ..... **Iliotona**
   Middle and hind tibiae with two basal teeth on a common process, teeth unequally spaced. Prosternum flat or convex, truncate or arcuate before 8
8. Prosternum fairly wide and flat, front edge truncate ..... **Hololepta** (s. str.)
   Prosternum narrower, partly convex, usually produced in a rounded point. Subgenus ..... **Lioderma**

Platyeutidium gen. nov.

Elongate-oblong, much depressed; black, shining. Front flat, smooth, toothed before eyes. Labrum rather large, bilobed. Mandibles with a single, obtuse tooth internally; robust, smoothly arcuate externally. Mentum subquadrate, transverse, slightly convex; truncate before, with a small tooth beneath each mandible. Prosternum broad, not narrowed before, flat, emarginate at sides before coxae, rounded at base. Mesosternum emarginate before. Propygidium flat; pygidium short, reflexed. Protibiae only obsoletely tridentate, teeth mere tubercles; tarsal groove deep, S-shaped, well defined.

Type, P. williamsi sp. nov.

This genus seems to be intermediate between Phylloma and Eutidium. In prosternal structure it is similar to the former genus, only the prosternum is not at all narrowed before in Platyeutidium. If differs further in that the mentum is truncate before instead of rounded as in Phylloma. The tubercles of the forelegs distinguishes it from any other known genus of the subfamily. In Eutidium, the mentum is emarginate and the prosternum broad at base and rather strongly narrowed before.

P. williamsi sp. nov.

Elongate quadrate, much depressed; black, shining. Front smooth, estriate, flat. Pronotum minutely puncticulate, no marginal stria present, a fine longitudinal striole present before scutellum. Elytra with subhumeral fossa deep at base, attenuate behind middle, sinuate; first and third dorsal stria fine scratches basally, 2nd a mere puncture at base; impunctate. Propygidium slightly convex, smooth except for a series of rather fine, close punctures at sides, and base. Pygidium short, inflexed, with a band of fairly fine punctures across base, apex smooth. Protibiae with 3 tubercles externally; middle and hind tibiae with 3 small teeth. Length (excluding, as elsewhere head and pygidia) 5 mm.

Type unique

Type locality; Kartabo, British Guiana, July 14th.

Named in honor of Dr. S. H. Williams, whose kindnesses to the author has made this paper possible.

P. unistriatum sp. nov.

Very elongate-oblong, very depressed; black, shining. Front without striae, flat, finely, scatteredly punctured. Pronotum minutely puncticulate, a fine antescutellar striole on basal half, no marginal stria present, but the sides convex, smoothly arcuate. Elytra minutely puncticulate, subhumeral fossa deep, sinuate, subentire, slightly attenuate apically, broad before base, a single, fine stria at base, one

quarter the length of the elytra, finely appendiculate; appendix as long as stria, punctiform. Propygidium convex, smooth, finely, sparcely punctate at sides. Pygidium recurved, densely punctate at base, impressed at center. Protibiae with 2 rounded tubercles. Mesotibiae and metatibiae tridentate, the teeth very short, scarcely visible. Length 4 mm.

Type, a single example, from Kartabo, British Guiana.

As this species was found with *williamsi*, it may prove that the two represent a single species, but as the differences are so many, it seems doubtful that the two specimens are merely sex variations. *Unistriatum* has an appendiculated elytral stria, the elytra puncticulate, the body much elongated, whereas in *williamsi*, the body is broader, the elytra smooth, with mere scratches for striation. In addition, the form of the subhumeral fossa, as well as the sculpture of the propygidia, are quite different.

Eutidium Lew.

As no synoptic table of this genus has as yet been published, the following one is included, prepared, in the main, from the original descriptions of the species. The writer follows Bickhart in sinking Orphinium into synonomy with Eutidium.

1. Front unarmed 2
   Front with a dentiform tubercle 11
2. Three dorsal striae present, 3rd often very short 3
   Two dorsal striae present 8
   Only one dorsal stria present; 5.5 mm. Brazil ..... **lepidum** Lew.
3. At least one apical appendix present 4
   None present 6
4. One apical appendix present; protibiae tridentate; 5–6 mm. Panama, **facetum** Lew.
   Two appendages present; protibiae quadridentate 5
5. Pygidium transversely punctulate; propygidium bi-impressed posteriorly. Front bistriate. First dorsal stria long; 9.5 mm. Brazil ..... **labrosum** Lew.
   Pygidium uniformly finely, densely punctate; propygidium convex, smooth, entoured by fine punctures. Front plain. First dorsal short; 4.5 mm. Brazil ..... **maragnoni** (Mars.).
6. First and second dorsal striae entire, 3rd short 5 mm. Brazil ... **pacale** Lew.
   All three dorsals short 7
7. Mandibles very large, prominent; epipleurae punctulate, almost smooth. Dutch Guiana. 8 mm ..... **mandibulare** Mars.
   Mandibles normal; epipleurae rugose; 6.5 mm. N. Granada ... **oblitum** Mars.
8. Propygidium with elevated line in middle. Protibiae 5-dentate; 9.5 mm. Ecuador ..... **exutum** Lew.
   Not so 9
9. Pygidium with posterior margin smooth; protibiae quadri-dentate. Pygidium uniformly punctate all over 10
   Protibiae three-dentate; 5 mm ..... **bahiense** Mars.
10. Mandibles obtusely but distinctly angulate externally; 7.5 mm. Columbia. **angulare** Lew.
    Mandibles arcuate smoothly externally; 6.75 mm. Peru ..... **peruanum** Lew.

11. Subhumeral fine, first dorsal appendiculate..... 12
Subhumeral very large, deepened at middle; first dorsal not appendiculate. Protibiae quadridentate, apical tooth bifid; 6.5 mm. Bolivia..**dentifrons** Des.
12. First longer than second, subentire, terminating apically in several points. Apical appendix very long, oblique, linear. Protibiae 4-dentate; 10 mm., **monodon**
First shorter than two. Apical appendix punctiform. Protibiae five-dentate; 8.5 mm. Brazil, Sao Paulo.....**tuberculatum**

Hololepta Payk.

In this genus, in addition to descriptions of several of new species, will be noted distributional records, some of which extend greatly the recorded distribution of species, as well as variations within species.

Subgenus **Hololepta** Payk.

H. (H). humilis Payk. Santarem, Brazil.

H. (H.). aradiformis Erichson. The appendix of the 1st dorsal stria varies greatly in length. Chapeda, Brazil; November.

H. (H.) quadriformis Mars. Chapeda, Brazil; November. Santarem, Brazil; May. Provinca de Sara, Bolivia; December.

H. (H). curta Mars. S. Paulo de Olivenua, Brazil; May. Taquara, Brazil; October. Santarem, Brazil; June.

H. (.H subhumilis Mars. Santarem, Brazil. Provinca de Sara, Bolivia; December.

H. (H.) attenuata Blanch. Rio de Janeiro, Brazil; November. Chapeda, Brazil; November. Santarem, Brazil; January. Para, Brazil. S. Paulo de Olivenua, Brazil; April.

H. (H.) columbia Mars. The single specimen of this species in the museum's collection differs from the typical form in having the two apical teeth of the protibiae on a common process instead of coming off singly and in the greater length of the appendix. Santarem, Brazil.

Subgenus **Lioderma** Mars.

H. (L.) quadridentata Fab. San Juan, Costa Rica. Chapeda, Brazil; October. Santarem, Panema and Macura, Brazil. Sao Paulo de Olivenua, Brazil; February and March. Kartabo, Brit. Guiana S. H. Williams collection.

The fossae of the anterior angles of the pronotum, in the males, varies from a small oval impression to the typical sinuous form.

H. (L.) clauda Mars. Guadalajera, Brazil.

H. (L.) mexicana Mars. Columbia.

H. (L.) minuta Erichson. Santarem, Brazil.

H. (L.) kahli sp. nov.

Oblong, subconvex; black, shining. Pronotum with a rather large fovea each side and disc basally, marginal stria entire, continued at base and ending before in shallow rounded impression, between the stria and margin a series of fine punctures apically. Elytra with

first dorsal short, second entire; subhumeral fossa apical, deep, abbreviated at base. Propygidium coarsely punctate around margin, more finely so apically, disc with scattered finer punctures. Pygidium densely, finely punctate. Protibiae, 4 dentate, middle and hind tibiae with lower ridge not toothed, above tridentate, the two apical teeth on a common process. Length 8 mm.

Type in Carnegie Museum; from Santarem, Brazil; unique.

Related to ***mexicanum*** Mars., but easily distinguished from it by the subbasal foveoles and the punctiform striole between marginal stria and edge on the pronotum.

Named in honor of Dr. Hugo Kahl, curator of entomology, at the Carnegie Museum.

H. (L.) braziliensis sp. nov.

Elongate oval, subconvex; black, shining. Front striate shortly, no sulcae between eyes. Pronotum minutely puncticulate; with marginal stria complete, continued at base and attaining fore angles; front angle in male indented; punctate coarsely before laterally. Elytra with first dorsal short, second broadly interrupted on basal half; subhumeral broad and deep, more narrow behind, abbreviated at both ends. Propygidium coarsely, sparsely punctate at sides, finely and more closely behind; disc finely punctate. Pygidium margined. Protibiae tridentate; middle and hind tibiae with inferior ridge coarsely bidentate, tridentate above. Length 8.5 mm.

Holotype ♂ Santarem, Brazil, June.

Allotype ♀ Chapeda, Brazil, September.

Types in Carnegie Museum.

Related to ***manillensis*** Mars., but the sculpture of the pronotum readily distinguishes it.

H. (L.) reichei Mars.

One specimen, with an additional fossa each side of the median and cephalad of the usual lateral fossa. The anterior pit of the pronotum is round and shallow, the subhumeral stria is short and apical. Perhaps this represents a new species but until more material is on hand the writer does not feel justified in naming it as it agrees so closely otherwise with ***reichei***.

Kartabo, Br. Guiana. S. H. Williams collection.

THE TARSAL CHEMORECEPTOR RESPONSE OF THE HOUSEFLY, MUSCA DOMESTICA L., TO SUCROSE AND LEVULOSE[1]

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For some years, it has been known that organs of taste are present on the mouth parts of some insects. More recently, however, it has been asserted that chemoreceptors, which perform the function of taste, are present on their tarsal segments. Minnich (1921) observed that certain nymphalid butterflies while walking over a substratum were able to detect food materials with which they came in contact. Following this, it was shown that a number of other insects possess chemoreceptors on the tarsal segments which perform the function of taste. This report presents a part of the work now being conducted on the tarsal chemoreceptor responses of the house fly to baits and the poisons used in them.

It has been demonstrated by Minnich (1922, 1926) that certain Lepidoptera and Diptera are able to detect sugar solutions by means of the chemoreceptors on their tarsal segments. Thresholds, mainly to sugars, have been determined for several insects which have extensible mouth parts by the use of proboscis movements as a criterion of response. Minnich (1929) working with the blow-fly, *Calliphora vomitoria* Linn., found that in the final stages of inanition the sucrose threshold of response in the most sensitive legs lies between 0.00004 molar and 0.00015 M with a more general threshold, however, between 0.00008 M and 0.00031 M. Crow (1932), in experiments on the sensitivity of the legs of certain *Calliphoridae* to sucrose, found the lowest threshold for *Lucilia sericata* Meigen to fall between 0.00031 M and 0.00125 M, for *Calliphora erythrocephala* Meigen, between 0.00015 M and 0.00062 M, for *C. vomitoria* Linn. between the values given by Minnich as stated above, and for *Cynomyia cadaverina* Desvoidy between 0.00004 and 0.00015 M. Both of these workers found that the threshold to sucrose falls during a period of water diet.

[1]Journal Paper No. J200, of the Iowa Agricultural Experiment Station, Project No. 136, State.

Experiments similar to those of Minnich and Crow show that the house fly, *Musca domestica* Linn., possesses chemoreceptors on its tarsal segments which perform the function of taste. Although these sense organs have not been detected morphologically, their presence appears certain on functional grounds. The investigation herein reported had as its purposes to show: First, that the house fly is able to detect the presence of sucrose in solution; secondly, to determine the average threshold of response to sucrose; thirdly, to determine some of the factors which affect this response; and fourthly, to compare the response of the flies to sucrose and levulose. No attempt was made to find the lowest threshold value; statistically, this value would be relatively uncertain. More attention was given to determining the average percentage of response at a definite age, 20 to 24 hours, in order to ascertain the concentration which would provoke a response when used in baits.

MATERIALS

The larvae of the flies were reared in food mixture similar to the one described by H. H. Richardson (1932) at temperatures between 29° and 33° C. In order to avoid the influence of ingested food, only unfed adults, 20 to 24 hours old were used. Flies of this age will readily respond to sucrose in solution and show less variation in feeding response than flies that have just emerged. It was necessary to regulate the number of flies reared in a container of media, as flies that were of small size, from overcrowding in the larval stage, were entirely unsatisfactory.

Granulated cane sugar was used in these experiments. Chemically pure sucrose was also tested as a check on any difference in the response that might be attributed to the impurities in cane sugar. Chemically pure levulose was used in paired experiments with sucrose in the form of commercial cane sugar in a study of a comparison of these two sugars.

Sucrose is a non-reducing, and relatively stable sugar. It does not ionize to any appreciable extent; consequently, its aqueous solution tends toward the neutral point. It can, therefore, be used with many poisons without reacting with them.

METHODS

A technique similar to the one used by Minnich (1929) was followed in mounting the flies which were to be used in the tests. Instead of employing ether to quiet the insects, however, they were subjected to temperatures low enough to render tham inactive so that they could be handled easily. The method of chilling was similar to that of Campbell, Sullivan and Jones (1934) who found a temperature of —1.1° C. for about 15 minutes to be satisfactory. This procedure was followed in order to eliminate any effects that might result from

ether anaesthesia. Number 9 wires about 4 inches long, to the end of each of which a cube of beeswax was fastened, were used as mounts for the flies. The flies were attached to the wax by their wings, while in the chilled condition, by melting the surface of the wax with a hot needle. All of the legs were left free. Unless otherwise stated, each fly so mounted was tested first on water and then on one sugar solution only, after which it was discarded. Repeated testing of the same individual fly was avoided to eliminate the possibility of fatigue of the chemoreceptors or any other possible influence of previous contact with a sugar solution.

The flies were divided into small lots, for the most part lots of ten, so that those which had been tested at different times and on different solutions could be treated easily from the statistical viewpoint.

The flies were brought into the laboratory, chilled in a refrigerator, mounted, and given time to recover fully from the effects of handling. Those which had obviously been injured in mounting, and those which did not regain the active use of their legs were discarded. Sucrose solutions were prepared fresh each day.

The experimental insects were tested first on distilled water. If they responded to water, they were allowed to drink until a response was no longer given; then, they were tested on another similar dish of water. If the flies were not responsive to water after repeated trials, it was assumed that they were water-satiated and that any subsequent response to a solution must be due to the presence of substances other than water. Each fly was then tested on a sucrose solution; the extension of the proboscis was taken as a positive response, and the failure to extend the proboscis as a negative response. Only full extension of the proboscis was considered a positive response; slight or erratic proboscis movements were recorded as negative responses. It is realized that the percentages of responses to a solution were lower than they would have been if just the slight movements of the proboscis were recorded as positive responses. As it is the purpose of these experiments to find the ratio of responses to sucrose which can be compared with similar ratios obtained with poison baits containing sucrose, the more evident criterion has been used. All of the experiments were made at room temperatures, between 25° and 30° C.

RESULTS

The conditions under which the flies were tested were purposely varied to reveal the effects of such factors as inanition, weight and age of the insects which might enter into the experiment and influence the results.

The effects of age and hunger upon the threshold of response to sucrose are shown in Table I. The threshold values were obtained by presenting first the solution of lowest concentration (0.0079 M) and proceeding to the next higher concentration until a response was given. The flies were not allowed to feed on any of the solutions. Immediately after emerging, 23 of

the 34 individuals tested, failed to give a response to 1 M sucrose solution. On the following day, however, a response to 1 M sucrose was given by all except four of the flies. These flies, likewise, would not respond to stimulation of the oral lobes which are more sensitive to sucrose than the tarsi. The table gives the threshold on the first day with the corresponding threshold that was obtained for each group 24 hours later,

TABLE I

THE EFFECT OF AGE WITH ITS INCREASE OF HUNGER ON THE RESPONSE OF THE STARVED HOUSE FLY TO SUCROSE

Range of Concn. Tested, Molar	Thresholds in Molar Concn. at 6 p. m. of day of Emergence	No. of Flies Responding	Thresholds in Molar Concn. Approximately 24 Hours Later	No. of Flies Responding
0.0079 to 1.0000	1.0000[a]	23	1.0000[a] 1.0000 0.5000 0.2500 0.1250 0.0625 0.0312	4 4 2 1 4 2 6
0.0079 to 1.0000	1.0000	3	1.0000 0.5000 0.2500	1 1 1
0.0079 to 1.0000	0.5000	6	1.0000 0.5000 0.2500 0.0312	1 1 3 1
0.0079 to 1.0000	0.2500	1	0.1250	1
0.0079 to 1.0000	0.0312	1	0.0156	1

[a]The thresholds of these flies were above 1.0000 molar which was the strongest concentration tested.

the groups being classified according to threshold on the first day. The results indicate that a 24-hour inanition period has a marked lowering effect upon the threshold of the tarsal chemoreceptor response to sucrose.

In order to show the effects of feeding on the threshold of response, 26 flies whose thresholds were 0.0625 M sucrose solution, were segregated and fed on a 1.0 M solution; they were tested again after a rest period of fifteen minutes. The

thresholds were now higher in every case except one. Nineteen of the flies failed to respond to a 1.0 M solution; two flies responded to a 1.0 M solution; three to a 0.5 M solution; and one to a 0.25 M solution. The threshold fell to a lower level again as the flies became hungry. The above untabulated data show very clearly that most of the flies, which have been permitted to feed, and are then tested after a brief interval, show a higher threshold to sucrose than flies which are held for a long period without food. This and the preceding group of experiments were the only ones in which the same flies were tested on more than one sugar solution.

TABLE II

COMPARISON OF RESPONSES TO COMMERCIAL CANE SUGAR WITH CHEMICALLY PURE SUCROSE

CONCN. OF SOLUTIONS MOLAR	COMMERCIAL CANE SUGAR			CHEMICALLY PURE SUCROSE		
	No. Flies Tested	No. Flies Responding	Percent Response	No. Flies Tested	No. Flies Responding	Percent Response
1.0	10	9	90	10	9	90
	10	8	80	10	9	90
0.25	10	10	100	10	9	90
	10	9	90	10	10	100
0.0625	10	7	70	10	6	60
	10	8	80	10	7	70
0.0156	10	4	40	10	4	40
	10	3	30	10	5	50

A few groups of abnormally large flies, from containers in which the food supply was over-abundant, failed to give responses to 1.0 M sucrose solution at the end of 24 hours. Some hours later, these same flies gave a threshold response comparable to that of flies of average weight at 24 hours. The importance of selecting flies which are standardized with respect to age and weight is indicated by these experiments.

An experiment was made to determine whether any significant difference occurred between the response to chemically pure sucrose and commercial cane sugar, which could be assigned to the impurities of the latter. To make a comparison over the entire range of the solutions used, four different concentrations were selected as shown in Table II. Flies from the same lot were mounted and divided at random into paired

groups. One group of the pair was tested on each of four concentrations of chemically pure sucrose, and the other group on the equivalent concentrations of commercial cane sugar. The resulting percentages of responses for the chemically pure sucrose and cane sugar did not vary significantly from each other or from those which had previously been obtained for commercial cane sugar.

Solutions of sucrose ranging from 1.0 M to 0.0039 M, were used in an investigation of the relation of sucrose concentration and ratio of response of fly populations. The dilutions were always made to one-half of the concentration of the solution

TABLE III

RESPONSES OF HOUSE FLIES TO SUCROSE

Molar Concn.	No. of Groups	No. Flies per Group			Percentage Flies Responding			X^2	P	Goodness of Fit
		Min.	Mean	Max.	Min.	Mean	Max.			
1.0000	21	5	9.8	15	60	91.6	100	28.332	.10–.20	Fair
0.5000	12	10	11.3	21	80	92.0	100	5.400	.90	Good
0.2500	15	10	10.7	17	60	80.8	100	13.491	.30–.50	Good
0.1250	4	10	10	10	80	85	90	.800	.80–.90	Good
0.0625	18	10	10	10	40	67.8	100	24.539	.10–.20	Fair
0.0312	12	10	10	10	50	56	70	3.100	.98	Good
0.0156	18	10	10	10	20	39.4	70	11.417	.80–.90	Good
0.0078	9	10	10	10	0	25	40	10.600	.20–.30	Good
0.0039	8	10	10	10	0	12.5	30	6.857	.30–.50	Good

next highest above it. The data from the replicated samples were used to test statistically the homogeneity of the responses of the flies to a given concentration. Table III shows the results of these tests. The minimum, maximum, and average percentages of responses are given for each concentration.

The chi-square test for homogeneity of the groups, used with each concentration, was calculated according to the method presented by Snedecor and Irwin (1933). The probabilities were taken from Fisher's (1930) table of chi-squares. Any values below .20 and above .10 were considered to indicate fair homogeneity. All values above .20 were considered good. All of the groups were found to be sufficiently homogeneous to prove that the responses were due to differences in concentration rather than to differences in the population samples.

The average responses to sucrose were found to differ little for the solutions of 0.125 M or above. Dilutions down to

0.125 M can be used in experiments on fly baits without meeting serious difficulty from the presence of an undue abundance of non-responding individuals. The fall of the response to solutions below 0.125 M was very rapid. Only one group gave a response below 80 percent for the 1.0 M solution. The 60 percent minimum response recorded for this concentration was erratic, in view of the other responses obtained, as the chi-square value will show. Responses to lower concentrations of sucrose were easily obtainable but, as previously stated, this investigation was chiefly concerned with the concentrations

TABLE IV

A Comparison, by Means of Paired Groups, of Responses of House Flies to Sucrose and Levulose

Molar Concn.	Sugar Tested	No. of Groups	Total No. Flies Tested	Total Responses	Percentages of Response		
					Min.	Mean	Max.
1.0000	Sucrose....	7	70	64	80	91.4	100
	Levulose...	7	70	51	60	72.8	80
0.2500	Sucrose....	9	90	69	60	76.6	90
	Levulose...	9	90	54	40	60.0	80
0.0625	Sucrose....	8	80	45	40	56.2	70
	Levulose...	8	80	33	20	41.2	60
0.0156	Sucrose....	9	90	32	20	35.5	50
	Levulose...	9	90	19	10	21.1	40
0.0039	Sucrose....	8	80	10	0	12.5	30
	Levulose...	8	80	4	0	5.0	30

of sucrose which would give a sufficiently high percentage of responses to be useful in poison bait experiments.

The point of 50 percent response to sucrose occurred at the approximate concentration of 0.025 molar. This value was read from a curve, fitted by eye to the mean percentages of responses plotted against the concentrations.

A comparison of responses of house flies to sucrose and levulose was made by means of paired groups. Flies from the same brood were separated at random into groups, one group being tested on a sucrose solution, the other on a levulose solution of equal concentration. The mean percentages of responses (see Table IV) were found to be significantly different for each concentration, a higher response being obtained with sucrose than with levulose. The ranges of the percentages of

responses are given. At all concentrations, except 0.0039 M, the range was higher for sucrose than for levulose. The chi-square test for homogeneity of the data from the 0.0039 M solution gave a probability between .30 and .50 for the sucrose and of .02 for the levulose; the latter figure indicates a discrepancy in the data for this concentration of levulose. Apparently the 30 percent maximum response obtained for levulose was higher than would normally be expected at this concentration. These data show that sucrose is more effective than levulose in stimulating the tarsal chemoreceptors.

SUMMARY

The tarsal segments of the house fly, *Musca domestica* L., are sensitive to solutions of sucrose and levulose. It is assumed that the responses to the sugars result from stimulation of chemoreceptor organs.

An average of about 10 percent of the fly population did not respond even to strong solutions of sucrose.

Flies which were permitted to feed gave a lower percentage of response than was given previous to the time of feeding.

Starvation increases the percentages of responses to sucrose solutions.

Commercial cane sugar and chemically pure sucrose were not significantly different in their effect on the tarsal chemoreceptor response of the house fly.

Levulose was less effective than sucrose in stimulating a response of the tarsal chemoreceptors.

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BIOLOGICAL STUDIES ON THE NITIDULID BEETLES FOUND IN PINEAPPLE FIELDS[1]

(Nitidulidae, Coleoptera)

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The Nitidulid beetles of pineapple fields are primarily scavengers of decaying plant wastes and have become very abundant coincident with the expansion of the pineapple in-

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dustry. In harvesting pineapples, only the fruit is removed while the leaves and stumps which have an extremely high content of sugars and starches remain in the fields to decompose. This decomposing material represents, in most cases, considerably more material than is harvested in the form of fruit. The stumps particularly, during decomposition, form an ideal environment wherein the beetles may breed.

The pineapple industry has been concerned by the great abundance of beetles in pineapple fields and desired to know what their real economic position might be. The information which was available at the inception of these studies was fragmentary and very unsatisfactory. The beetles were thought to attack the growing plant and to be capable of direct injury.

The association of the beetles with decomposing pineapple trash suggested that they might actually be beneficial in hastening decomposition. This has been considered critically. Control has purposely been avoided since there is no immediate need for control and such studies would be a separate research project in itself.

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I. LITERATURE SUMMARY

Literature references to the biology and economic significance of the Nitidulidae found in pineapple fields are not numerous. Since they are brief, the significant statements can be quoted as they appear. Illingworth (11) said, "Carpophilus is a genus of beetles with very numerous species in Hawaii. Several years ago some of the commoner exotic forms came into the limelight because of their abundance about the canneries. Though this trouble was soon overcome by better sanitary methods, conditions have gradually become worse in the fields. From my investigations I have come to look on these beetles as major pests. They undoubtedly cause a loss of many thousands of dollars annually. While they have always been recognized as pests of the ripe fruit, I find that they begin their ravages on the young plants as soon as they are put in the ground. Furthermore, they attack the green fruit, even when it is as small as a walnut. Though the beetles tuck their eggs far down among the scales or into cracks in the soil, the ants, with their constant patrol, search them out, and thus keep

the pests somewhat in check. Moreover, Pheidole feeds on both the grubs and the adults on every possible occasion."

Illingworth (12) said, "Souring Beetles, (Nitidulidae). There are about five exotic species found in pineapple fields. The most troublesome and abundant is *Carpophilus humeralis* Fab. These beetles are pests of the plant at every stage of its growth. Starting when the planting material is put into the soil, they congregate on the butts, gnawing on the starch material between the fibres, they oviposit there and the developing grubs frequently cause the breaking down of the plant by feeding at the base of the lower leaves, where rot fungi are introduced. When abundant they gnaw cracks between the lower eyes of the fruit followed by fermentation."

Illingworth (13) said, "Five cents per fruit is paid as a bonus for fruit in the cannery with larvae on them." "Refuse dumped about the cannery is the source of the beetles." "The best results for the industry can only be secured by the strictest sanitary field practice. It is there that the insects breed and clean culture will go far toward removing these insects in the cannery."

The afore-mentioned statements, in general, are not in agreement with the findings of the present paper. Since experimental evidence is lacking in these papers, direct criticism is not justified.

Carpophilus hemipterus, which is a cosmopolitan species, has received considerable attention because of its relation to endosepsis or souring of figs and also because it is a pest to the dried fruit industry. An excellent summary of this problem as well as considerable original information was given in 1931 by Simmons, Reed and M'Gregor (21). The beetles act as mechanical carriers of endosepsis of figs. They are also responsible for the dissemination of the organisms causing fig smut. Phillips, Smith and Smith (18) included rotting apples, old prunes, cull grapefruit, nectarines, raisins, peaches and rotting oranges in the food list of the beetles. Hagan (9) in a report of a trip to Turkey discussed the relation of *C. hemipterus* to endosepsis of figs in that region. Essig (6) gave a short account of the life history and control of the beetle in California.

Williams (26) gave a short account of the Hawaiian species and notes that they are found in association with broken fermenting stalks of cane.

De Ong (5) added some information without actual data on the effects of cold storage on the beetles which had infested raisins but this has no bearing on the field problem as it is encountered in Hawaii.

II. THE SPECIES OF HAWAIIAN NITIDULIDAE AND THEIR DISTRIBUTION

Six species of Nitidulid beetles, *Carpophilus hemipterus* (L.), *C. humeralis* (Fab.), *C. dimidiatus* (Fab.), *C. maculatus* Murray, *Haptoncus ocularis* (Fairm.) and *H. mundus* Sharp, are found in the pineapple fields of Hawaii. There are, so far known in Hawaii, 138 species of Nitidulidae in the indigenous fauna of the Islands but these are not encountered in pineapple fields (20). They are restricted to the forests in the mountains and are not ordinarily seen. The species of Car-

pophilus are all probably introduced species with the exception of *C. maculatus* which has not been recorded from other parts of the world. *Haptoncus ocularis* is common in the East Indies but *H. mundus* is only recorded from the Hawaiian Islands. There is no record to indicate when the introduced species arrived in Hawaii. There is a likelihood that some of them may have been here before the advent of modern commerce since they are common in a variety of foodstuffs and may well have been transported by pre-historic peoples. *C. hemipterus* and *C. humeralis* are the commonest species, the other two Carpophili being found only rarely. *Haptoncus ocularis* is quite common in fermenting fruits but seldom becomes markedly abundant. *H. mundus* is rare under all circumstances.

The literature records of the distribution of the Nitidulidae found in Hawaii must be considered with caution in view of the long list of synonyms which are given for each species. The present determinations are probably correct since a series of each species was sent to the British Museum to be compared with type specimens or with specimens of authentic determination. The following records of distribution are considered to be valid. The authority for each locality is given in parentheses.

Carpophilus humeralis (Fab.). India, Africa, Mauritius, Hawaiian Islands, (20). Madagascar, Tropical Africa, Seychelles, East Indies, (8). China, (25).

Carpophilus hemipterus (L.). Cosmopolitan, (20). North America, Mexico, British Honduras, Guatemala, (19). California, (21). Papeete, (15).

Carpophilus dimidiatus (Fab.). Cosmopolitan in stored food products.

Carpophilus maculatus Murray. Hawaiian Islands, (20). Polynesia, (16).

Haptoncus ocularis (Fairm.). Hawaiian Islands, East Indies, (20).

Haptoncus mundus Sharp. Hawaiian Islands, (20).

The ability of these beetles to live on decaying plant materials coupled with the great increase of inter-continental shipping in recent years, makes it highly probable that they are distributed to many other regions and not as yet recorded. Systematic literature is notably behind the times in listing the faunas of various localities and the absence of authentic references of distribution is certainly not an indication that the species are limited to the regions which have been listed.

III. REGARDING THE RELATIVELY RECENT INCREASES IN THE NUMBERS OF CARPOPHILUS BEETLES IN HAWAII

The appearance of *Carpophilus humeralis* in large numbers must be of recent occurrence. Sharp (20) states that it was not abundant in collections. In describing its habitat he mentioned that it was taken in the Waianae mountains at high elevations and was also recorded from Honolulu. While he made no specific mention of it being found in relation to pineapple or sugar cane, it is felt that he would not have considered it a rare species had he been able to obtain as large and unlimited series as may be collected in the pineapple fields at the present time. This would also seem to be the case with *C. hemipterus*. He mentioned it as occurring in foodstuffs and made no other mention of

its habitat. It would appear that the increase of these species is in some way related to the favorable conditions for breeding which are found in pineapple fields, particularly the older or abandoned ones.

The species of *Haptoncus* were also relatively rare according to Sharp's observations. *Haptoncus ocularis* was mentioned as being found on Oahu, Hawaii, Kauai and Lanai. *H. mundus* was recorded from Oahu, Hawaii and Kauai.

IV. THE ECONOMIC SIGNIFICANCE OF THE NITIDULID BEETLES IN HAWAII

It is a very difficult problem to evaluate properly the true economic significance of the nitidulid beetles found in pineapple fields. Probably their greatest importance in causing losses is a very indirect one in that they may be classed more as a nuisance than as a true economic pest. They do represent a minor cannery problem when they are at all abundant since they occasionally find their way into the canned fruit in the packing lines. Over-ripe fruits containing beetle larvae may also contaminate sound fruit after it has gone through the Ginaca machine.

A letter of inquiry asking for specific information as to the number of complaints they had received from consumers finding beetles in their canned products was sent to all of the canneries in the Islands. The replies to these letters were extremely variable. All of the canneries recognized that the beetles constituted a nuisance and all of them were aware of the fact that they occasionally found their way into the cans during the processing of the fruit. Complaints are very unreliable as indications of the frequency of the presence of beetles in the cans because the retail merchant does not pass the complaint to the packer unless the complaints are of unusual frequency. The presence of a beetle or two in an occasional can of fruit, while not desirable from the standpoint of good merchandising, does not affect the quality of the fruit. It remains an open question as to how great the real losses from beetle contamination would be in actual practice.

Cannery practices in regard to the beetles vary considerably. One of them pays bonuses to the girls in the packing line for every fruit they find with beetle infestation. Some pay no particular attention to the problem. One company reports that the frequency of beetle infested fruits is greater in winter when the intervals between picking dates are greater. Fruits which become over-ripe develop breaks between the carpels which attract the beetles. Shorter intervals between picking reduce the amount of over-ripe fruit and thus also reduces the amount of beetle infestation. Only one company had actual information as to the number of times beetles were encountered in the packed fruit. In the course of inspection work during a seven-month period this cannery reports that of 9705 cans opened, beetles were found in 8 cans. Of these, one can was of sliced fruit and the balance was of crushed. Out of 1697 cans of juice examined a single can was found with a beetle in it. Certainly the very infrequent appearance of beetles in packed fruit does not merit any special attempts to control them in the field.

The disposal of cannery wastes would be of some importance in control of beetles. If these wastes are dumped in the immediate vicinity of the cannery they provide suitable places for the beetles to breed and thus constitute a certain menace. The utilization of waste in various by-products such as pineapple bran eliminates this problem to a large extent. Good sanitary practice, which is desirable for other reasons, is the greatest factor in keeping the beetle population in and around the canneries at a low level.

V. EVIDENCE SHOWING THAT THE BEETLES ARE NOT THE PRIMARY CAUSE OF ANY KNOWN INJURY TO PINEAPPLE

In the review of literature it was pointed out that there have been numerous opinions that nitidulid beetles are capable of causing a variety of types of direct injury to the pineapple plant. In this present study it is considered that all such statements which are not backed by actual experimental data are valueless. It is true that *Carpophilus hemipterus* is a vector of certain pathogens of the fig fruit in California, but no strictly parallel diseases are described for pineapple. The mere presence of any insect in large numbers does not necessarily imply that it is a pest though it might be classed as a nuisance.

The evidence showing that the beetles are secondary rather than primary in their attacks on pineapple falls into several distinct categories. These are based on: (a) The general field picture, (b) The known food habits of the beetles, (c) Actual tests to produce primary injuries under controlled conditions.

(a) *The General Field Picture*

The field picture of the relation between the Nitidulidae and diseased conditions of the pineapple plant can be approached best by first considering the circumstances under which they are found in the pineapple fields. They are found associated with almost every injury of the pineapple plant which is characterized by necrosis or rotting. This excludes certain leaf rots which become dry and are not suitable as breeding places except under very specialized conditions.

The most common type of fruit injury where the beetles are found is that provisionally called intercarpellary rot of ripe fruit. This cannot, in a strict sense, be termed a disease since it seems to be a stage in the normal decomposition of the fruit. It is characterized by breaks in the fruit surface between the carpels and does not appear until the fruit is beyond the stage where it would normally be harvested. The beetles are attracted to these breaks in the fruit by the juices that ooze out. Other insects, notably drosophilid flies, are attracted to these same places coincidently with the beetles.

"Leaky fruit," a condition induced by large populations of mealy bugs in ripening fruits (1), also attracts the beetles. This type of injury is becoming more rare as the control of mealy bugs progresses. Examinations of a large series of fruits at Kahuku on Oahu in plots which had not been sprayed for mealy-bug control revealed that beetles were almost universally associated with leaky fruits.

Fruits which have been injured by the gnawing of rats always harbor large numbers of beetles and drosophilid flies. These fruits are generally too badly injured to be of any use commercially. Fruits which are bruised or broken in picking and are allowed to remain in the field are included in types of miscellaneous injuries which attract the beetles. When such fruits are left in the field for even a short time beetles find entrances and soon ruin the fruit completely. Immediate transportation to the cannery obviates a total loss from this type of injury.

All of the injuries which have been described have some other primary cause, the beetles being found secondarily. Whenever an insect is spread over a considerable area as is the case of the Carpophilus beetles in Hawaii, it is reasonable to suppose that primary injuries due to them will also be distributed in a similar fashion. Carpophilus beetles are found wherever pineapples are grown in the Hawaiian Islands but there seems to be no relation between the distribution of the beetles and any type of plant failure. Beetles are found in pineapple fields of all ages from the time they are first planted until after they have been removed from production and are ready for a new planting. If the beetles were the cause of damage either by direct feeding or as the vector of any disease, such hypothetical injuries would probably be general in distribution and frequent of appearance coincident with the general distribution of the insect.

(b) *The Known Food Habits of the Beetles*

The evidence which is gathered from the known food habits of the beetles does bear considerable weight in showing that they do not initiate plant injuries. The Carpophilus species concerned in this study, namely *C. humeralis* and *C. hemipterus*, are scavengers on all types of decaying plant materials. They have been described from sugar cane as feeding on stalks which have broken and started to ferment (26). They are found in decaying fruits, both in commercial plantings and in the mountain forests. In pineapple fields they are always found associated with decaying plant parts or in places where fermentations or necrosis have started as a result of other causes. In searching for methods of rearing these species the author was misled by statements in the literature which would lead one to suppose that it would be possible to rear beetles on any portion of the pineapple plant. Experience has definitely shown, however, that it is impossible to rear the beetles on any fresh materials, though they will develop readily if there is any decomposition. The female beetles will not oviposit on fresh materials and seem capable of retaining matured eggs until they find a suitable place to oviposit. If the females are kept on sterile media or in containers without food, they never lay eggs, but if put with decayed materials they begin to oviposit within a few hours and continue throughout their normal life if mating is frequent.

(c) *Actual Tests to Produce Primary Injuries Under Controlled Conditions*

The third type of evidence is the most conclusive. To obtain this, beetles of both species were caged on representative parts of the pine-

apple plant and observed until their death. These experiments merit a detailed description which follows. *Carpophilus humeralis* and *C. hemipterus* were the species tested since the frequency of appearance of the other species is very low as will be indicated in the discussion on field sampling.

(1) *Tests to induce feeding on fruits.*—Beetles of both species were caged on both green and ripe fruits. The method of caging was simple, being a small vial set in a plaster of paris mold so that a fruit surface the area of the mouth of the vial was exposed to the beetles. This method permitted observation of closely delimited portions of the fruit and facilitated careful examination of controlled areas on the fruits. Plaster of paris had the advantage of not causing any surface necrosis of the fruits unless it was left for periods far beyond the life of the beetles used in the experiments. Waxes and wax compositions were also tried but were very unsatisfactory because they tended to break down the surface of the fruit within a few days. Ten *C. humeralis* and 10 *C. hemipterus* were put into each vial. It had become apparent from a series of previously unreported experiments that there would be no feeding by either species. No food was supplied to the beetles since it would have been a source of unwanted contamination. Water from condensed moisture within the vials was at all times available to the beetles. No special source of ventilation was necessary since the vials were loosely fitted in the plaster of paris molds and it was apparent from the continued activity of the beetles within the vials that they were not suffering from lack of oxygen. These cages were set up in replications of 10 to 15 dependent on the immediate availability of material.

In the tests on green fruits the beetles were unable to penetrate the surfaces even under the drastic treatment of prolonged starvation. When this evidence is compared with conditions in the field where food materials are always present it is certain that if the beetles could attack the unbroken fruit surfaces they would under the conditions of enforced starvation. Examination of the caged fruit areas showed that the beetles did make attempts to feed or perhaps to escape but could do no more than remove the waxy surface coat leaving the cell walls uninjured.

In the case of ripe or over-ripe fruits there were several instances where the beetles did penetrate between the carpels. A significant thing, however, was that similar areas of intercarpellary rots were found in sufficient number on other portions of the fruit so that it was impossible to ascribe entrance of the beetles to their own penetrating ability but rather to the chance appearance of the rot on the caged portions. In all cases where the fruit as a whole remained sound the beetles did not penetrate it. The location and frequence of these intercarpellary rots over the surface of the fruits was so general that they might be expected to appear at the particular places where the cages happened to be placed. Fruits with the intercarpellary rots were sectioned, the lesions were compared with those where the beetles had penetrated and were found to be similar. If, as was the case in a few instances, the beetles were allowed to remain in the lesions for several days after penetration it was found that there was a greater fermenta-

tion due, no doubt, to the fact that the beetles carry a veritable flora of micro-organisms on their bodies and inoculate the lesions more efficiently than would be the case if the fruit were not exposed to the beetles. This is in agreement with the information obtained from the canneries which shows that the numbers of fruits thrown out because of beetle infestation bears a direct relation to the stage of ripeness and the frequency of picking. If the fruits are left in the fields beyond the initial ripeness there is a normal breakdown which the beetles penetrate. If the fruit is picked at short intervals and sent to the cannery immediately there are few "throw-outs," but if the intervals between pickings are extended to two weeks or more, as is sometimes the case in winter, the number of "throw-outs" in the packing line increases.

(2) *Tests to induce beetles to feed on green leaf tissues.* Beetles were caged on green leaves in various stages of growth in vials secured by strong rubber bands. Sufficient water to meet the requirements of the beetles was condensed on the wall of the vial. No food material was supplied. Approximately 10 beetles of each species were put into each of the vials and every trial was repeated at least 10 times. These beetles were caged 10 days before they all died from starvation. The results were negative in all cases. The beetles made no attempt to feed on the leaf surfaces nor were they able to chew their way through in an attempt to escape. The results of these experiments were so decisive that it seems inconceivable that the beetles would ever attack leaves in the field where other more suitable food materials were obtainable.

A variation of this experiment was used in which the leaf tissue beneath each cage was scarified with a sterile needle before the beetles were introduced. In every case the leaves developed symptoms of Thielaviopsis rot. Checks were set up at the same time in which the leaves were scarified but no beetles put on them. In 50% of the checks symptoms of Thielaviopsis rot appeared at about the same time as in the cages with beetles. This would be expected since the rot organisms are omnipresent. The only difference was that the presence of the beetles made the inoculation certain. If these checks had been run under field conditions the natural inoculation would probably have been even higher.

(3) *Tests to induce beetles to feed on white tissues at the bases of leaves.*—Beetles were caged on white tissues at the base of leaves. These tissues are newly differentiated and are extremely soft in comparison with those which have developed chlorophyll. The method of caging was similar to that of the previous experiment. In no case were the beetles able to penetrate even these soft tissues nor did they even attempt to feed on them. These tender tissues are very compact and are not exposed and are not readily accessible to the beetles but there are avenues of entrance in almost every plant. Even though the white tissues are partially exposed in the growing plant, they are not attacked by the beetles even when the latter are present in large numbers in the fields.

(4) *Tests to induce beetles to feed on sterile stump surfaces.*—Beetles were exposed to sections of stump which were kept in a relatively

sterile condition with a weak solution of sodium fluoride. This solution was too weak to kill the beetles but it did inhibit the growth of decay organisms. The beetles fed on the open stump surfaces and in some cases actually penetrated them. In the field, however, broken stumps seldom occur so that this does not become an important source of infection for the growing plant. Certain economic losses due to rot during the curing of the crowns, slips and suckers may be attributed to the beetles if they have access to the broken surfaces before the plant has had time to form a cork layer. It was not within the province of this study to determine the relation of the beetles to the occurrence of butt rot, but there is a suggestion that they may be a greater factor than has heretofore been considered. They do have the ability of penetrating open butt surfaces and they are capable of carrying rot organisms on the surfaces of their bodies.

(5) *Possibility of beetles feeding on outer stump surfaces.*—No tests were made of this portion of the plant since the outer stump surfaces are much harder than the other portions of the plant and there is no reason to suppose that the beetles would be able to attack them when they fail to penetrate much softer tissues.

VI. LIFE HISTORY OF CARPOPHILUS HUMERALIS (FAB.)

No references were found in the literature which would give any clue to the life history of *Carpophilus humeralis*. Even though this beetle was very abundant in the pineapple fields, its habits were little known. The results of this phase of the study help to explain why such large numbers of the beetles can be present in the field.

(a) *Preferred habitat of the beetle.—Carpophilus humeralis* is a scavenger of all types of decaying plant materials. In the fields such materials are generally the stumps of pineapple plants which have been broken down and allowed to decay in the preparation of the field for a new crop. The beetles are not restricted to the pineapple plant, however, but may be found in any plant material which is in the process of decomposition. They will not reproduce on living plant materials as was previously shown by repeated trials.

(b) *Mating.*—The mating of the beetles is very frequent. Females do not lay eggs until after mating has occurred. If a female is allowed to mate she will lay eggs for several days but the number of eggs laid gradually diminishes and finally ceases. If she is again permitted to mate the production of eggs commences once more.

(c) *Oviposition.*—The female beetles are very selective in the choice of places to oviposit. They lay their eggs either on or in decaying plant material. Females were kept in glass dishes without laying a single egg but oviposited within 24 hours if suitable materials were supplied to them. Various soils were also tried but the females refused to lay eggs in them unless fairly large particles of decomposing material were present.

Detailed records were kept of the oviposition of 25 females. These females were put in Petri dishes containing squares of pineapple stump and since the eggs were laid beneath the stump they could be removed

and counted with a high degree of accuracy. New stump material was added and the old material removed at intervals because it was impossible to recover the eggs if the stump became too decomposed. The females used were newly emerged from laboratory breedings and were observed during their entire lives. No temperature record was kept since it was found that the females were but little influenced by the slight fluctuation of temperature in the laboratory. Table I and Fig. 1 show the relation between temperatures and the numbers of eggs laid by eight females over a short period during which the food

TABLE I

Numbers of Eggs Laid by Eight Females of *Carpophilus humeralis* (Fab.) per Day with the Corresponding Maximum, Minimum and Mean Temperatures for Those Days

Number of Eggs Laid	Maximum Temperature	Minimum Temperature	Mean Daily Temperature
61	26.5° C.	22.5° C.	24.5° C.
117	26.0	22.5	24.3
153	26.5	23.0	24.8
148	27.0	23.5	25.3
2	29.0	24.0	26.5
67	27.0	21.0	24.0
78	23.0	21.0	22.0
91	21.0	21.0	21.0
81	21.0	21.0	21.0
94	26.5	22.0	24.3
112	26.0	22.0	24.0
40	28.0	21.5	24.8
97	28.5	22.0	25.3
143	29.0	21.0	25.0
130	26.0	20.5	23.3
89	28.0	18.5	23.3
9	27.0	19.5	21.8
0	24.5	17.5	21.0
62	25.0	19.0	22.0
85	25.0	18.0	21.5
103	27.0	19.5	21.8
76	27.5	21.5	24.5
79	28.5	21.5	25.0

medium was changed several times. The nature of the medium on which they deposit their eggs is, in this experiment, by far the most significant controlling factor in determining the number of eggs which a female will lay during any given period.

The averages of 25 pairs of beetles are shown in Table II. The highest number of eggs laid by any of the females during her life was 1466 or an average of 14.66 eggs per day for the active egg laying period. This particular female was unusually fecund since she produced the phenomenal number of 58 eggs within one 24-hour period. Her unusual capacity becomes more striking when it is realized that the estimated volume of the eggs laid during this 24-hour period exceeded

the volume of her abdomen. The figures in the table show that there is a considerable variation in the reproductive capacity between individuals, but in general there is a fairly close relation between the length of life of a female and the total number of eggs laid. Except for the very short-lived females the average numbers of eggs laid per day is fairly similar.

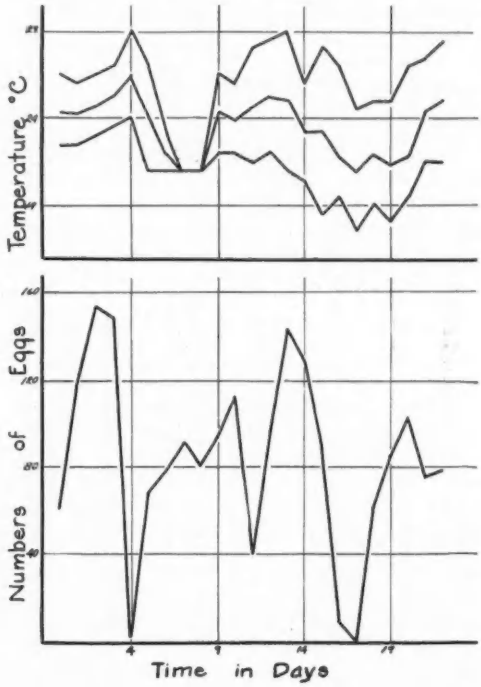

FIG. 1. Numbers of eggs laid by eight females of *Carpophilus humeralis* (Fab.) compared with the maximum, minimum and mean temperatures for those days.

Detailed records of five selected females of the group are given in Table III. These records are supplied to give the reader a greater detail of what is represented in the mean figures of the summary (Table II) and also to emphasize further the influence of the nature of the medium on the numbers of eggs laid on any given day. It is seen from this table that there were 25 females under laboratory conditions from this table that there were very significant decreases in the numbers of eggs laid following the replacement of the medium.

These oviposition records, however, cannot be considered as characteristic for conditions in the field. There, the conditions are entirely

different and to a large degree dependent on the weight of the population in the immediate environment. The beetles tend to congregate in large numbers in decaying pineapple stumps. In some instances over 6,000 beetles were counted from a single stump. In the laboratory similar conditions of crowding were produced and in these cases no eggs were ever seen. This is also borne out in field observation. Some larvae are nearly always found in association with a dense population of

TABLE II

Oviposition, Preoviposition and Postoviposition Periods. Numbers of Eggs Laid and Length of Life of Females, in Days, of *Carpophilus humeralis* (Fab.).

Female No.	Length of Life	Preoviposition Period	Postoviposition Period	Oviposition Period	Total No. of Eggs Laid	Average per Day	Maximum per Day
1	91	4	0	87	1384	15.90	50
2	93	6	2	85	824	9.69	50
4	98	9	2	87	924	10.62	32
5	112	8	4	100	870	8.70	27
6	105	7	5	93	1086	11.68	46
7	113	10	28	75	761	10.15	25
8	78	6	2	70	689	9.84	41
9	76	6	6	64	688	10.75	30
10	29	8	0	21	82	3.90	14
11	40	5	3	32	331	10.34	26
12	104	8	3	93	1267	13.62	37
13	113	6	12	95	1101	11.59	40
15	111	7	4	100	1271	12.71	41
16	110	8	16	86	1026	11.93	37
17	23	7	2	14	190	13.57	22
18	94	24	4	66	971	14.71	32
19	81	7	3	71	821	11.56	41
20	90	6	0	84	1073	12.77	36
21	111	6	5	100	1466	14.66	58
22	86	6	1	79	972	12.30	30
24	48	6	1	41	568	13.85	36
27	111	6	6	99	854	8.63	27
28	112	6	16	90	1006	11.18	37
29	98	10	2	86	882	10.26	34
30	94	5	9	80	948	11.85	38
Av.	88.84	7.48	5.44	75.92	882.2	11.47	35.48
Max.	113	24	28	100	1466	15.90	58
Min.	23	4	0	14	82	3.90	14

beetles, but the number is relatively small in comparison to the numbers which might be present on the evidence of the oviposition records. This indicates that there is within the species itself a factor which tends to reduce its numbers. This particular characteristic is, however, not unique for this species but is a characteristic of all animal populations. The exact manifestation of the factor or factors within the species which tend to limit its numbers may vary but the end result is the same.

TABLE III

Record of Deposition of Eggs of *Carpophilus humeralis* (Fab.) on Pineapple Stump Material, Honolulu, 1932

Date of Oviposition	Eggs Laid by Female, No.					Date of Oviposition	Eggs Laid by Female, No.				
	5	6	13	15	21		5	6	13	15	21
April 4	....	....	....	....	....	May 24	18	36	6	33	58
5*	†	†	....	....	....	25*	15	46	17	33	35
6	0	0	....	....	....	26	3	18	4	2	8
7	0	0	†	†	....	27	24	11	22	18	17
8	0	0	0	0	†	28	24	11	22	19	18
9	0	0	0	0	0	29	20	4	17	16	24
10	0	0	0	0	0	30	20	10	15	18	22
11	0	0	0	0	0	31	23	11	20	30	12
12	0	0	0	0	0	June 1	10	7	40	15	15
13*	0	1	0	0	0	2*	15	17	14	34	10
14	9	15	8	0	0	3	14	7	0	3	7
15	3	17	6	13	2	4	7	9	0	1	0
16	8	23	0	0	1	5	10	3	1	1	0
17	13	19	7	14	0	6	10	3	1	2	0
18	9	24	0	10	10	7	23	2	11	10	0
19	10	25	16	8	8	8	13	8	3	8	0
20	11	18	29	25	13	9	10	7	4	5	2
21*	12	13	24	12	7	10	20	18	0	8	5
22	0	9	0	0	0	11	14	22	7	19	8
23	7	21	8	10	15	12	4	11	1	3	5
24	9	32	13	6	21	13	4	11	0	3	5
25	15	29	9	15	15	14*	5	12	1	3	4
26	14	29	31	14	25	15	2	8	0	2	0
27	12	29	5	9	17	16	0	0	9	7	39
28	11	24	23	12	9	17	11	0	23	23	37
29	10	19	27	7	13	18	14	17	24	36	54
30	15	0	23	5	12	19	7	14	34	40	48
May 1*	6	0	12	0	9	20*	7	15	34	40	49
2	9	2	9	0	16	21	4	7	6	6	3
3	0	7	0	0	9	22	0	23	16	3	37
4	0	0	20	8	8	23	9	2	23	34	24
5	5	0	17	0	13	24	14	2	32	12	29
6	2	3	17	8	38	25	7	34	35	26	31
7	2	3	18	8	39	26	0	9	39	26	8
8	5	11	20	9	28	27*	0	9	40	26	8
9*	5	12	21	10	29	28	0	7	1	8	0
10	0	0	0	0	0	29	27	16	32	18	20
11	0	0	4	0	0	30	6	17	14	15	11
12	5	4	15	0	23	July 1	11	21	1	16	10
13	5	12	10	8	30	2	12	21	1	16	10
14	0	3	6	15	16	3*	8	2	3	10	23
15	7	24	16	22	26	4	3	0	0	9	0
16	7	24	17	23	27	5	7	8	0	17	0
17	0	14	2	8	10	6	15	10	0	23	9
18*	0	31	10	19	8	7	21	7	0	41	6
19	0	0	6	7	3	8	24	3	9	10	10
20	15	13	6	0	16	9	24	2	8	10	9
21	6	14	18	8	37	10	7	2	6	25	5
22	23	12	11	19	49	11	7	1	5	25	4
23	13	5	0	28	56	12	15	3	14	14	0

TABLE III—[*Continued*]

Date of Oviposition	Eggs Laid by Female, No.					Date of Oviposition	Eggs Laid by Female, No.				
	5	6	13	15	21		5	6	13	15	21
July 13*	14	1	1	11	0	21	1		0	7	1
14	0	0	0	3	0	22	0		0	7	1
15	0	0	0	9	4	23	0		0	0	0
16	0	0	1	18	15	24*	0		0	0	0
17	1	0	0	10	23	25	‡		0	0	0
18	1	‡	0	10	22	26			0	0	0
19	1		0	7	2	27			0	‡	‡
20	1		0	7	1	28			‡		
						Total.....	870	1086	1101	1271	1466

* Indicates replacement of stump material.
† Emergence date of female.
‡ Death date of female.

(d) *Longevity.—Carpophilus humeralis* is comparatively long lived. Records of the length of life of 25 females under laboratory conditions is given in Table II. In this determination the true limits of longevity have not been shown since some factor causing a premature death ended the experiment before the true distribution of mortality could be obtained. The longevity of the 25 females is shown in Fig. 2 which indicates from its skewness that some factor induced premature death of some of the individuals. This is too small a number from which to expect a very good frequency distribution of mortality, but the chart does suggest that some of the beetles can live for longer periods than those indicated in the experiment. The males, in general, seem to be less hardy since most of them died very prematurely and had to be replaced by others in order that mating might take place at frequent intervals.

(e) *Length of the immature stages.*—The detailed study of the various stages of immaturity was undertaken to get a general idea of its nature rather than to make a finished study of all the details throughout a whole range of temperatures. The beetles were reared individually in small shell vials at a constant temperature of 27° C. The food used was a bit of decomposing pineapple stump. It is an extremely difficult thing to rear these beetles to maturity. The preliminary records are characterized by failures rather than successful rearings. Most of the deaths occurred during larval life. No explanation can be offered for the premature death of the larvae. The prepupal period is not always clearly defined though it is generally fairly easy to determine because the mature larvae wander about in search of a place to pupate. The records of lengths of immature stages for 12 males and 12 females are given in Tables IV and V, respectively.

The length of the egg stage is more than one day and less than two days at the temperature used. The active feeding period is nearly a day longer on the average for those larvae destined to become males.

TABLE IV

Length in Days of the Immature Stages of *Carpophilus humeralis* (Fab.). Males at a Constant Temperature of 27° C.

Length of Immature Stages				Total Time of Immaturity
Egg Period	Feeding Period	Pre-pupal Period	Pupal Period	
2	4	11	5	22
2	4	11	5	22
2	7	6	5	20
2	4	7	6	19
2	4	9	6	21
2	4	6	6	18
2	4	8	6	20
2	6	6	6	20
2	6	10	5	23
2	6	10	5	23
2	6	10	5	23
2	6	5	6	19
Av. 2	5.1	8.3	5.5	21.0

TABLE V

Length in Days of the Immature Stages of *Carpophilus humeralis* (Fab.). Females at a Constant Temperature of 27° C.

Length of Immature Stages				Total Time of Immaturity
Egg Period	Feeding Period	Pre-pupal Period	Pupal Period	
2	4	8	5	19
2	7	5	6	20
2	4	10	5	21
2	4	9	5	20
2	4	10	4	20
2	5	6	6	19
2	4	7	6	19
2	7	9	5	23
2	6	4	6	18
2	6	5	5	18
2	6	4	6	18
2	7	9	5	23
Av. 2	5.3	7.2	5.3	19.8

The pupal period is similar in length for both sexes while the total length of the immature stages is a day longer for the males than for the females. It is very likely that this difference may be due to coincidence and would disappear in a thorough investigation. Variations in the length of the various stages are certainly to be expected, it being impossible to control the nutrition of the larvae because variation in the micro-flora of the stump material supplied would completely alter the availability of the food constituents to the larvae.

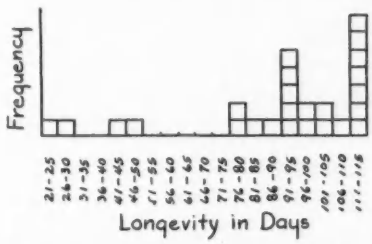

FIG. 2. Distribution of the longevity of 25 females of *Carpophilus humeralis* (Fab.)

VII. LIFE HISTORY OF CARPOPHILUS HEMIPTERUS (L.)

The life history of *Carpophilus hemipterus* has been worked out by Simmons, Reed and M'Gregor (21) and bears a close similarity to that of *C. humeralis*. It differs in details but agrees in that this species is also one with a relatively short larval period, a long adult life and a high potential of reproduction. In pineapple fields the two species have the same habitat. There may be differences which favor one species to the detriment of the other as is suggested when quasi-quantitative samples are taken of field populations.

VIII. DISCUSSION OF LIFE HISTORY DATA

The facts of the life histories of *Carpophilus humeralis* and *C. hemipterus* give an insight into the reasons for their great abundance. They are species which have a high potential of reproduction. The length of the immature stages is fairly short under average field conditions. The length of adult life is long in comparison to the larval life. The number of suitable habitats for the beetles is large, consisting of 15 to 20 tons of decomposing stumps per acre. With these facts in mind it can readily be seen that with such favorable conditions the beetle populations will always be at a high level unless field practices are modified to remove the decomposing stumps as a habitat for the beetles. Shredding or burning the plants in fields removed from production are both possible means of removing the habitats. If shredding is resorted to, it is essential that the final material be fine enough to be dried at the soil surface or plowed under and completely covered so as to put it out of reach of the beetles which do not actively dig in the soil in search of food. Controls of this sort, however, cannot be

expected to do much good unless they are a widely practiced measure. Both *Carpophilus humeralis* and *C. hemipterus* are extremely mobile species which are attracted from considerable distances by decomposing material and unless the suggested practices were followed over the whole area of an island little effect could be expected. It must also be remembered that there are large quantities of decomposing material, even in actively growing fields, which is a suitable environment for the beetles. Some of this could hardly be removed economically. Control would seem to be inadvisable unless at some time in the future the beetles should become the vectors of some wide-spread disease.

IX. THERMAL DEATH POINT OF CARPOPHILUS HUMERALIS

It was frequently observed that on hot days in the field, soil surface temperatures became high enough to throw the beetles into dormancy and that death sometimes ensued. This might well have been a limiting factor in the distribution of beetles. A few determinations of the

TABLE VI

Thermal Death Points of *Carpophilus humeralis* (Fab.) as Determined from Laboratory Experiments

Temperature	Number Tested	Exposure Time	Percent Mortality
53.9° C.	50	10 min.	100
50.8	50	10	100
48.6	50	10	99
48.3	50	10	99.5
48.1	50	10	97.5
46.7	50	10	6.5
46.4	50	10	0

thermal death point of the beetles were made to be compared with soil temperature records to see if temperature was an important limiting factor. Small bolting cloth cages which could be slipped into vials in a water bath at controlled temperature were made. The beetles were exposed in these for periods of ten minutes and then brought back to room temperature and mortality determined after five hours. The results are given in Table VI. Complete mortality will occur at 50.8° C. at an exposure time of 10 minutes. When this is compared with the records of soil temperatures taken at Wahiawa, Oahu, by Hagan (10) it will be seen that the soil surface temperatures never reach a lethal level for the beetles. At a depth of ¼ inch there are sometimes periods when the temperatures are definitely at a lethal level.

These comparisons might be significant if the beetles were not able to escape from the areas of high temperatures. Actual observations made in the field indicate that it is very unusual for the beetles to expose themselves to these high temperatures. When the soil surface temperatures rise to a level too high for their comfort they escape by taking flight or by seeking refuge on vegetation or plant debris where

the temperature is not detrimental. Massed flights of the beetles are often seen on days when the temperatures at soil level are high. This is the general explanation for finding large numbers of the beetles on young plants. The soil in pineapple fields generally contains enough decaying plant material to support a fair population of the beetles and when the soil temperature goes above the toleration point they seek refuge in other strata where the temperatures are not so extreme.

TABLE VII

Records of Periods When Soil Temperature at One-fourth Inch Depth would be Lethal to *Carpophilus humeralis* at Wahiawa, Oahu
(Data taken from Hagan (10).)

Date	Time	Maximum Temperature
July 16, 1931.....	2:00 P. M.	53° C.
July 17, 1931.....	2:00 P. M.	55
July 18, 1931.....	2:00 P. M.	55
July 20, 1931.....	2:00 P. M.	51

X. PREDATORS WHICH MAY ACT ON CARPOPHILUS BEETLES

No authentic parasites are recorded for any of the Nitidulid beetles found in Hawaii. Numerous predacious species are found in the stump associations, the most important of which is probably ***Pheidole megacephala*** (Fab.). None of the predators are particularly efficient in reducing the numbers of beetles in the field. Pheidole ants will attack both the larvae and adults of the beetles under experimental conditions but apparently they are not particularly active in searching for them. An opportunity for observing the action of Pheidole was found in the trash heap at the Experiment Station at Wahiawa. Both beetles and larvae were extremely abundant in the decomposing material and Pheidole nests were unusually numerous. The significant thing about the observations made here was that pupae of the beetles were found in great abundance within ¼ inch of the established runways of the ants. Apparently the ants do not utilize the beetles for food unless they actually encounter them. Pheidole ants do not actively search for the beetles even when the immature stages of the beetles are extremely abundant.

Hydrophilid beetles of the genus *Dactylosternum* may be of some importance as predators on the larvae found within rotting stumps. Several important factors act, however, to inhibit the efficiency of these predators. They are only found under circumstances where the interior of the stumps is very wet, that is, semi-liquid. The other factor is the tremendous capacity of the host beetles to produce eggs. In nature the factor of crowding prevents the Carpophilus beetles from giving full expression to their ability to reproduce and the relatively small number of larvae which a predator may destroy in no way tends to limit the numbers which actually survive.

XI. QUANTITATIVE STUDIES OF THE POPULATIONS OF NITIDULID BEETLES IN PINEAPPLE FIELDS

There is a growing tendency in the literature of entomology to place emphasis on the need for quantitative methods of studying insects. It is necessary, first of all, to consider what sort of problems may be attacked from this approach. It is apparent that quantitative methods are nothing more than a tool, and every tool has certain purposes to which it may be put and others where its use is either very inefficient or else entirely unsuitable. The use of the method depends entirely on the point of view as to what are considered the important things to know about an insect species and this will vary with the particular species with which we concern ourselves. There is no single method by which we can analyze an insect problem any more than there is a universal method of analysis in the field of chemistry. If we wish to know how an insect population varies from place to place or from time to time or with one treatment as contrasted to another the quantitative approach is certainly a valid one. It must be recognized that there are many biological problems which do not fall within these categories. Quantitative methods certainly are not a panacea for the unknowns in biology any more than they are in the fields of physics and chemistry which have used the quantative method with its helpmate of mathematics for a long time.

Mere counting and tabulating alone does not imply that the method used is quantative unless this sort of information is gathered for the entire universe in question. In biology it is seldom possible to describe a universe within limits small enough to be worked with as a whole. There have been some cases where this has been done, notably the work of Chapman and his colleagues (2) with *Tribolium confusum* Duv., in which the limits of the environment are definite and predetermined. Pearl (17) in working with populations of Drosophila in a milk bottle was able to work with an entire population whose limits of environment could be so controlled that the individuals in it could be subjected to actual count. In the field the limits of the environment cannot be defined and it is necessary to resort to samples or aliquots of the population. When this is done, a method cannot be truly quantitative until enough samples have been taken to measure statistically whether the universe is homogeneous or heterogeneous and what degree of variation may be expected from a given number of samples. If the limits of error cannot be defined the mere presence of numerals in tabular form cannot be expected to confer automatically some magic virtue of reliability to the data or make it quantitative. It is not held that a poor numerical estimate may not be better than one that is only stated in qualitative expressions of a vague nature, but it is necessary to be aware of the fact that with a very heterogeneous distribution the numerical expression may be no better than one expressed in terms of adjectives unless it can be shown that the numerical expression does not have a wide range of error due to randomness of sampling. The distinction must be made between a truly quantitative method and a qualitative method expressed in quantitative terms.

Data expressed in terms of the numbers of individuals per unit area, whether it be a square millimeter or square mile may also be very misleading in insect ecology. The true habitat of Nitidulids in pineapple fields is not the entire area over which they are distributed but rather the micro-environment represented by decaying pineapple stumps or other decomposing matter. The beetles do not distribute themselves homogeneously over an entire area at random but tend to aggregate in these stumps in a semi-gregarious fashion, attracted and held together mainly by the food that is represented in the stumps. The beetles have, as has been shown, the ability to reproduce at a rate which enables them to be constantly in competition among themselves for the food and space which is available in these smaller environments. Thus, the numbers of beetles given in terms of a unit area which is not a natural one will not become necessarily an expression as to the true weight of their population within the micro-environment but rather an expression of the number of environments where they can live within that area, which, when it is properly considered, does not tell us anything about the populations of beetles within these particular micro-environments but tells us only the approximate frequency of the environments. This can be obtained by simpler methods than counting the beetle populations per unit area.

The use of certain types of baits and traps may also lead to erroneous conclusions unless they are used with caution. Simmons et al. (21) used traps baited with rotting peaches in an attempt to control *Carpophilus hemipterus* in California and found that the numbers of beetles which were taken in the traps did not vary with the numbers of beetles in the area but was dependent on the maturity of the fig crop. When there were no figs for the beetles to feed on or breed in, the trap catches were fairly high, but as soon as the figs reached maturity they competed with the traps in attractiveness and though it could be seen that the beetle populations had actually increased many fold, the evidence of the traps was certainly not true evidence. Instead of measuring the weight of the beetle populations in this case it measured the state of maturity of the figs. This again was not the object which was sought.

In the preliminary studies on the populations of Carpophilus beetles in pineapple fields a similar observation was made. Pineapple stumps were put out at the edge of a ratoon planting with the idea of collecting them at a later date and counting or estimating the populations represented in these trap stumps. In the intervening interval the trap stumps were examined but not collected and found to have fairly large numbers of beetles associated with them. A day later the company decided to break down this particular ratoon field in preparation for replanting and when the trap stumps were collected they were found to have only a negligible number of beetles. Most of them had been attracted to the adjoining field where the food materials were more attractive than the trap stumps. Obviously the trap stumps in this instance were not at any time a true index to the beetle populations in the area.

Another disconcerting feature of the attempts to sample the beetle populations was the inability to handle the material obtained since even with the smallest of baits the numbers of beetles caught was far beyond human ability to segregate to species and to tabulate their numbers. The use of aliquots of the sample was suggested and tried. Instead of getting the true estimate of the sample it was found that the error of the aliquot was superimposed over the error of the sample itself so that the analysis of the area on that basis would be very misleading and little better than guesswork.

TABLE VIII

Summary of Mean Values of Field Samples Taken at Brodie, Oahu

Date	Carpophilus humeralis	Carpophilus hemipterus	Carpophilus maculatus	Haptoncus ocularis	Haptoncus mundus
May 17, 1933	44.08%	54.07%	0.94%	0.25%	0 %
May 24, 1933	39.38	56.80	3.05	0.11	0.14
May 31, 1933	25.71	71.38	2.48	0.12	0.23
June 9, 1933	26.31	68.75	4.11	0.07	0.05
June 23, 1933	12.50	86.58	0.92	.....	.....
July 7, 1933	57.23	41.85	0.51	0.02	0
July 19, 1933	71.86	27.57	0.31	0.01	0.01

Date	Staphilinidae	Colobicus parilis	Crypto-morpha desjardinsi	Carpophilus dimidiatus	
May 17, 1933	0.61%	0 %	0.06%	0%	.....
May 24, 1933	0.54	0	0	0	.....
May 31, 1933	0.09	0	0	0	.....
June 9, 1933	0.65	0	0.08	0	.....
June 23, 1933	0.02	.....	0	0	.....
July 7, 1933	0.36	.....	.....	0	.....
July 19, 1933	0.25	0.01	.....	.....	.....

Some plant ecologists have made use of a theory which has been given the name of "Raunkaier's law of frequence" (Summarized by Kenoyer (14).) and have stated that the per cent frequency with which a species was found in a long series of samples could be translated into actual numbers per unit area. This was investigated to see if it had any possibilities for the present problem. This method may be of some use for comparison in certain plant environments but the theory breaks down in cases where the samples are large enough to contain at least one individual of each of the species with which we are concerned. It was impossible to apply this theory to any of the samples which could be obtained in pineapple fields since both of the important species were always present in the samples even where it was known that they existed in very unequal ratios. The first three species would in nearly all cases give a per cent frequency value of 100 but the ratio in which they are actually present in the samples varies from less than 0.0001 to more than 0.9000.

The method of sampling finally used cannot be considered to be quantitative entirely even though it does have certain quantitative aspects. It has been observed that there seemed to be some relation between the age of a knocked down pineapple field and the ratios of *Carpophilus humeralis* and *C. hemipterus* which were present and the time which had elapsed since the field was worked with a stump cutter. *C. hemipterus* seemed to be the more frequent at the earlier stages and seemed to be replaced by *C. humeralis*. To determine whether this was a safe generalization, a series of samples was taken on a field transect at intervals of about ten paces. These samples were not taken with the idea of being able to compute the number of beetles per unit area but rather to gain a qualitative knowledge of the frequencies of

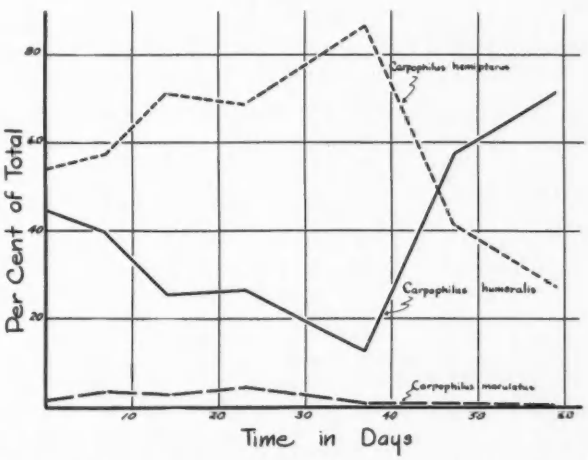

FIG. 3. Mean percentages of Nitidulid beetle species in a field of decomposing pineapple trash at Brodie, Oahu.

the two species over the field. The beetle content of one or more stumps was taken at every sampling point. This was a simple thing to do since it was found that if a stump was disturbed either by striking it or by cutting into it that most of the beetles would crawl out of it and could be collected readily in a jar with an ordinary funnel. In some cases it was not feasible to collect all of the beetles which were found in a stump but this was not an important source of error since it was found that there was a very close similarity between the ratios of the species whether only a fraction of them were collected or if the entire beetle content of the stump was taken. Usually the number of beetles per sample varied between 100 and 1000. If more than this number were taken in the samples the labor of segregation into species became too burdensome. This method of sampling was very crude at best but it was possible to show certain trends in the ratios of species by its use.

These samples tell nothing about the actual abundance of the species with which we are concerned.

In addition to the Nitidulidae, certain other Coleoptera were taken by this method of sampling. *Colobicus parilis* Pasc. (Family Colydiidae) and *Cryptomorpha desjardinsi* (Guer.) (Family Cucujidae) were recorded as well as a number of undetermined species of Staphylinidae which are considered as a group. Several species of *Dactylosternum* were not uncommon in the stumps but they were not collected in the samples since they cling tenaciously to the trash and do not drop off as do the other species. Various species of *Drosophila* flies were also present but were not considered since they could not be collected by this method of sampling. Numerous other species were taken as separate

TABLE IX

Summary of Mean Values of Field Samples Taken at Kunia, Oahu

Date	Carpophilus humeralis	Carpophilus hemipterus	Carpophilus maculatus	Haptoncus ocularis	Haptoncus mundus
May 21, 1933	17.77%	76.82%	1.13%	3.51%	0.57%
May 28, 1933	33.12	64.19	1.38	0.92	0.19
June 23, 1933	62.12	30.66	5.14	0.83	0.70
July 5, 1933	14.48	82.40	1.56	1.20	0.20
July 18, 1933	48.65	49.77	0.74	0.58	0.19

Date	Staphilinidae	Colobicus parilis	Crypto-morpha desjardinsi	Carpophilus dimidiatus	
May 21, 1933	0.15%	0 %	0.09%	0%	.....
May 28, 1933	0.14	0	0.02	0	.....
June 23, 1933	0.25	0.11	0.19	0	.....
July 5, 1933	0.08	0.07	0.01	0	.....
July 18, 1933	0.05	0.04	0.01	0	.....

individuals but most of them could not be considered as being associated with decomposing pineapple trash.

Samples were taken at Kunia, Galbraith and Brodie on Oahu at different periods and were continued in each field until samples could no longer be gathered either because of the completion of decomposition in the field or because of the inability to find sufficient numbers of beetles to give a reliable index of the ratios of the species. The results are expressed as the ratios of the various species to the total numbers. This is given as a percentage value. The mean values are summarized in Tables VIII, IX and X and are graphed in Figs. 3, 4 and 5.[2] Variations between samples are very great, so great, in fact, that the

[2]Detailed analyses of all of the samples on which these summaries are based are given in a thesis of the same title as this paper on file in the library of the University of Hawaii.

decimals of the percentages are of no significance whatever. Their only purpose is to show the frequency of the lesser species.

The analysis of the ratios of the species of beetles found in decaying pineapple stumps shows that there is no common generalization which can be drawn from the evidence. There is a tendency for *C. humeralis* to be less frequent during the initial stages and to be more frequent at the time the last samples were taken. By this reasoning it must follow that *C. hemipterus* is the most frequent at the initial stage and less frequent at the end. This takes no account of the lesser species. They are seen to go through minor fluctuations and always remain at low frequency. The populations of the two major species in a given

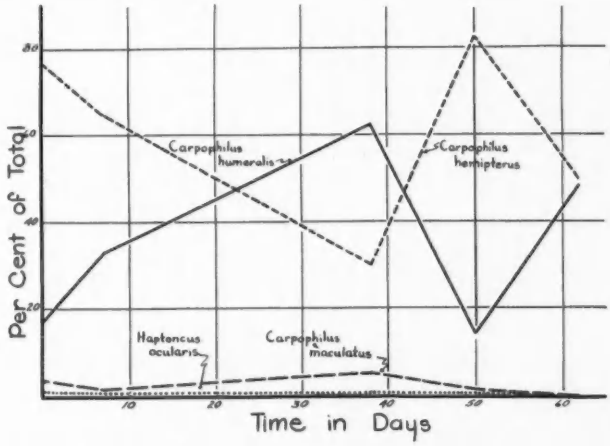

FIG. 4. Mean percentages of Nitidulid beetle species in a field of decomposing pineapple trash at Kunia, Oahu.

area are not determined by reproduction since it is very apparent that the violent fluctuations which are shown occur in shorter periods than the life cycles. Both species are extremely mobile and the numbers of a species that are found in an area are determined by the attractiveness and fitness of that environment. Migrations to and from the area occur readily so that the populations of the unit environments are very unstable which makes it impossible to apply such reasoning as Volterra (23) suggests in his theoretical approach to the explanation of fluctuations in animal populations. Volterra's proposition considering any number of species competing for the same food suggests that all of the species will tend to decrease save that for which the coefficient $\frac{\epsilon}{\tau}$ is the largest. ("Toutes les especes s'epuisent sauf celle dont le $\frac{\epsilon}{\tau}$ est le plus grand."). In this coefficient ϵ is the coefficient of increase and τ is the coefficient of voracity. In the present case the population

numbers are determined mainly by the attractiveness of a particular unit environment in comparison to adjoining ones and neither of the aforementioned coefficients is of much importance in determining what the population will be in the unit environments in a field of decomposing stumps.

TABLE X

Summary of Mean Values of Field Samples Taken at Galbraith, Oahu.

Date	Carpophilus humeralis	Carpophilus hemipterus	Carpophilus maculatus	Haptoncus ocularis	Haptoncus mundus
Mar. 23, 1933	9.70%	84.41%	4.80%	0.35%	0.18%
Mar. 30, 1933	25.88	63.86	9.58	0.27	0.15
April 5, 1933	29.42	57.45	12.58	0.24	0.15
April 12, 1933	51.17	40.05	7.37	0.33	0.07
April 19, 1933	64.34	25.27	6.57	3.28	0.09
April 26, 1933	54.04	19.65	9.10	15.91	0.30
May 3, 1933	37.15	43.29	5.20	13.08	0.77
May 10, 1933	54.45	40.70	2.09	1.79	0.34
May 17, 1933	85.22	12.49	1.24	0.51	0.01
May 24, 1933	91.44	7.10	0.86	0.24	0.05
May 31, 1933	85.59	11.56	1.85	0.24	0.12

Date	Staphilinidae	Colobicus parilis	Crypto-morpha desjardinsi	Carpophilus dimidiatus	
Mar. 23, 1933	0.49%	0.02%	0.01%	0.01%	.....
Mar. 30, 1933	0.22	0.02	0	0	.....
April 5, 1933	0.12	0.03	0.03	0	.....
April 12, 1933	0.89	0.06	0.02	0	.....
April 19, 1933	0.37	0.09	0	0	.....
April 26, 1933	1.14	0.03	0.01	0	.....
May 3, 1933	0.48	0.06	0	0	.....
May 10, 1933	0.58	0.04	0.02	0	.....
May 17, 1933	0.05	0	0	0	.....
May 24, 1933	0.31	0	0	0	.....
May 31, 1933	0.10	.....	0	0	.....

XII. DECOMPOSITION OF PINEAPPLE STUMPS AS AFFECTED BY THE PRESENCE OF NITIDULID BEETLES

The observed presence of large numbers of Nitidulid beetles in decomposing stumps of the pineapple plant suggested that instead of being an outright nuisance the beetles might be an important factor in the decomposition of plant residues remaining in a field broken down in preparation for a new planting. None of the previous studies on decomposition of pineapple material had considered the presence of the beetles and experiments in decomposition had been set up so as to eliminate the beetles as a factor. Allen and Abel (Unpublished) compared stumps which had been inoculated with micro-organisms which beetles carry with those which had received the natural inoculations

from soil alone and found that there was a slight difference in the rate of decomposition in favor of the beetle inoculations. Their work, however, was done with a small number of stumps and there was no way of deciding whether the results were truly significant nor have they made any claims of significance. The composition of pineapple stumps is known to be extremely variable. This would require that any experiment to show the true influence of the beetles would have to be based on the composite of a large number of stumps subjected to treatment with and without beetles. To overcome the handicap of variability it was necessary to set up the experimenton as large a scale as would come within the physical ability of collecting and analyzing the material and at the same time be of sufficient volume to overcome the errors

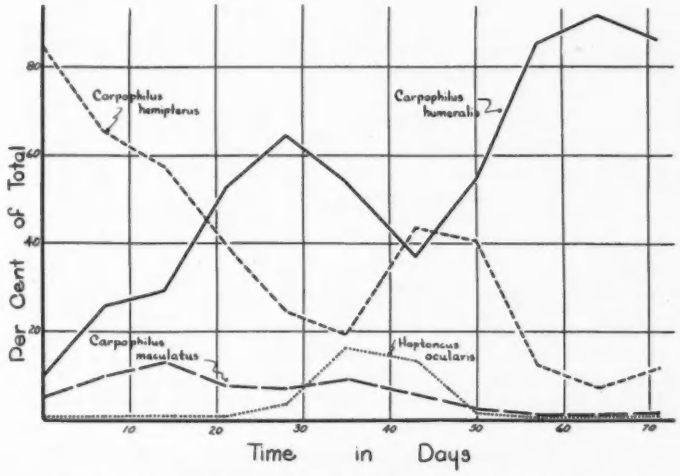

FIG. 5. Mean percentages of Nitidulid beetle species in a field of decomposing pineapple trash at Galbraith, Oahu.

of random sampling. Only the stumps of pineapple plants were used since ordinarily Carpophilus beetles are not directly associated with the decay of leaves.

(a) *Methods and materials.*—The stumps were collected from a ratoon field at Brodie on Oahu. The leaves and axillary roots were trimmed from the stumps which were tagged, and weighed on a balance which gave an accuracy of 1 gram. Thirty-one of these stumps were dried and the average moisture content was calculated to obtain an estimate of the moisture content of the entire group. The remaining 300 stumps were put into screened cages from which it was possible to exclude all beetles. These cages had a 6-inch layer of soil on their floors. Two of the 4 cages used were kept free of beetles while the other two had a generous mixed population of beetles added to them.

The cages with beetles were not sealed so that beetles from the wild could enter the cage as well. No attempt was made to control any of the incidental species of insects which may have been associated with the soil since it was felt that such limitations would make the experiment too artificial and not comparable to field practices. No claim is made that the conditions within the cages were exactly comparable to the field because, obviously, by the nature of the experiment it was not possible to exclude the beetles from the cages and at the same time have the conditions similar to those outside the cage.

Samples of approximately 30 stumps were drawn from each of the two series of cages at intervals of two weeks. These were dried and the dry weight losses recorded. This material was then ground in a Wiley mill and stored to be analyzed later for losses of chemical fractions.

TABLE XI

Decomposition of Pineapple Stump Material With and Without Beetles Measured in Terms of Dry Weight Losses. The Tabulated Values Represent the Actual Per Cent Loss

Date	Without Beetles		With Beetles		Difference	Standard Deviation of the Difference
	Mean	Standard Deviation	Mean	Standard Deviation		
Dec. 23, 1933	0	.....	0	.....	0	0
Jan. 6, 1934	23.98±1.20	9.930	25.99±1.28	10.248	2.02±1.76*	.....
Jan. 20, 1934	36.40±1.46	11.866	40.01±0.83	6.622	3.61±1.68*	2.490
Feb. 3, 1934	47.73±1.12	9.100	56.49±0.88	6.987	8.71±1.42	2.107
Feb. 17, 1934	54.91±1.22	9.927	62.37±0.74	5.886	7.46±1.43	2.183
Mar. 17, 1934	63.31±0.77	6.182	66.45±0.41	3.301	3.14±0.87	1.297

* These differences are not statistically significant since they fall well within the range of error of random sampling.

The original dry weight of the stumps was an estimate based on the dry weight of 31 of the original stumps. This method was found to give a mean that gave an accuracy within 0.848 per cent of the true mean which was more than sufficiently reliable for this type of analysis. The mean dry weight was 35.62 ± 0.420 per cent of the original wet weight and on this basis the estimated original dry weight of all of the stumps was obtained. When this estimated figure is applied to the individual stumps it does not give the true original dry weight of that stump but it does give a good measure of the dry weight of samples of 30 stumps such as were drawn at the various stages of decomposition. The estimated dry weights of all of the stumps were calculated and a measure of variability was obtained for each of the sample series after decomposition. This particular statistical treatment may not be entirely valid but it does give an approximation of the reliability of the differences which were found between samples with and without beetles. This estimated significance is the best that can be obtained from this type of experiment and even though it is not the true measure it is better than no estimate at all.

The stumps were dried at a temperature of approximately 70° C. for 4 days. This did not drive all of the water from the material since it has been found that complete dryness is not to be obtained even at a temperature of 105° C. With this material, however, such a temperature would alter the nature of the sugars by caramelization and render them useless for chemical analysis.

(b) *Results of analysis on the basis of dry weight loss.*—The presence of beetles in the decomposing pineapple stumps was found to influence decomposition to a degree that was significant statistically but not significant from the aspect of practicability in speeding up decomposition in actual field practice. A summary of the analyses of stumps in various stages of decomposition is given in Table XI and graphed in Fig. 6.[3]

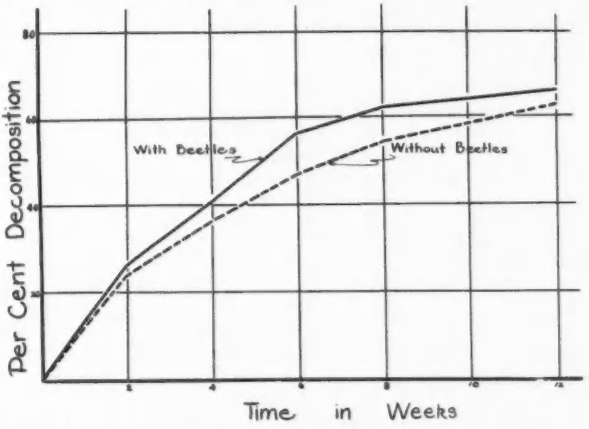

FIG. 6. Decomposition of pineapple stumps with and without beetles measured in terms of dry weight loss.

It is seen that the losses measured on a dry weight basis give consistent results indicating that this method of analysis is a reliable measure of decomposition. The influence of the beetle is, in all cases, a definitely measurable one but the differences do not become truly significant until the sixth week of decomposition. At 6 weeks the greatest difference of 8.71% appears after which time the difference between the 2 treatments decreases. The tendency is toward having them come together again so that any gain in decomposition which was due to the beetles was lost when the total dry weight losses became of the order of 60%.

At the time the experiment was closed the stumps were reaching the point where they were no longer a suitable habitat for the beetles.

[3]Detailed analyses of the stumps on which these summaries are based are given in a thesis with the same title as this paper filed in the library of the University of Hawaii.

At that time both the materials with and without beetles were very similar and it can be concluded that the end results take place at approximately the same rate in both.

(c) *Methods of Analysis of the Fractions*

(1) *Alpha-cellulose.*—It would have been desirable to have made the analysis for cellulose on the basis of the total cellulose content but the technical difficulties involved made it necessary to be content with only the alpha fraction. All the standard methods for the quantitative analysis of cellulose call for a series of filtrations through sintered crucibles of Jena glass. This method may be very satisfactory for wood pulps and bagasse but the cellulose of the pineapple stumps was of such consistency that it clogged the sintered glass crucibles making the analysis difficult and of doubtful value. A new method was devised following, in general, the method of Gortner and McNair (7) which

TABLE XII

Decomposition of Alpha-cellulose in Pineapple Stump Material With and Without Beetles.
(Tabulated figures give the estimated per cent remaining.)

Time in Weeks	Without Beetles	With Beetles
0	21.28%	21.28%
2	21.00	17.59
4	19.12	18.24
6	18.96	17.19
8	19.75	17.98
12	17.35	15.51

was entirely adequate for the alpha-cellulose fraction but not for the beta and gamma cellulose. Since this method is partly original it will be described in detail.

One gram of dried material was triturated with 17.5% sodium hydroxide for ½ hour and then diluted to give a solution of approximately 4%. The alpha-cellulose precipitates at this stage. To eliminate filtrations at this point the solution is centrifuged and the supernatant liquor is siphoned off. The residue is diluted with water and the precipitate is again thrown down in the centrifuge. This is repeated until the liquor gives a test for neutrality. The cellulose is then treated with a 10% solution of acetic acid which is washed out by successive dilutions to neutrality. A few drops of ammonium-hydroxide are added to the last washing. The residue is transferred to porcelain crucibles and dried for 8 hours at 105° C., after which the crucibles are transferred to a desicator to cool before weighing. The crucibles are then put into a muffle, ignited, removed to a desicator to cool and weighed once more. After this the ash is removed and the crucibles are finally weighed to determine the tare. This method

substitutes separation by centrifuging and decantation for filtration and does not invalidate the theory of the accepted method of Gortner and McNair (7) and has the advantage of making it possible to work with materials that would clog the crucibles used in the standard methods. If the material is too finely divided there may be slight losses due to the fact that the finer particles of cellulose may be lost in not coming down as a precipitate. This loss was negligible for the present analyses where the purpose was to arrive at an estimate of decomposition losses of the alpha-cellulose fraction rather than to arrive at a critical determination of the exact amount of cellulose present.

No great accuracy can be claimed for this method of analysis since the time of treatment with the sodium hydroxide may be a profound factor in influencing the yield of alpha-cellulose. It was pointed out by Gortner and McNair that successive treatments of the same material

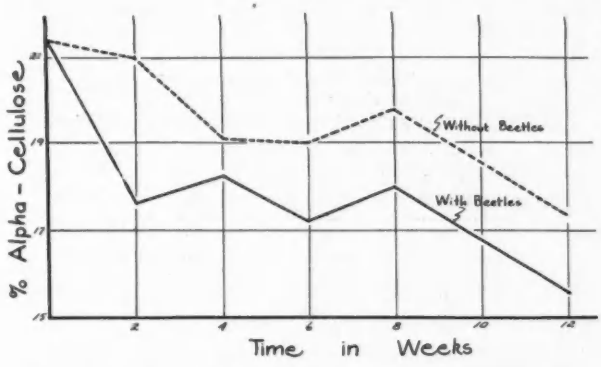

FIG. 7. Decomposition of alpha-cellulose in pineapple stumps.

by their method gave very appreciable lowering of yield. All that can be claimed is that the method gives an approximation for indicating trends.

(2) *Ether soluble extract.*—The ether soluble fractions were determined by taking a small quantity of dried material from each sample and extracting with anhydrous ether in a Sohxlet extraction apparatus for 16 hours. The ether was then evaporated and the residue weighed. (Official Methods of A. O. A. C. p. 279–280, (22).)

(3) *Sugars.*—The sugars were determined as invert sugar by the method of Munson and Walker. This method is standard and so well known that it requires no further discussion. (Official Methods A. O. A. C. p. 281, (22).)

(4) *Starches.*—The starches were determined by treating the residues of the sugar extract with pangestin, determining the sugars formed by the method of Munson and Walker and then calculating the amount of starch from the dextrose equivalent by multiplying the amount of dextrose obtained by the factor 0.90. (As recommended in the Official Methods of the A. O. A. C. p. 282, (22).)

(d) ***Decomposition of alpha-cellulose as influenced by the presence of Carpophilus beetles.***—The effect of the presence of Carpophilus beetles on the alpha-cellulose fraction of pineapple stump material is shown in Table XII and Fig. 7. The data as presented are not without considerable variability due in part to the method of analysis and in part to the heterogeneity of the material which was used in the study. The results are consistent in showing that the decomposition of alpha cellulose is accelerated by the presence of the beetles but not to the extent that would be desirable from the standpoint of field practice. The chemisty of decomposition of cellulose itself is not sufficiently known and so no significance can be placed on the slight increase of alpha-cellulose at the end of 6 weeks of decomposition. This result may be due to the inherent error of the method of analysis or it may mean that the beta and gamma cellulose fractions are converted into the alpha form before they are hydrolyzed into sugars.

TABLE XIII

Decomposition of Total Sugars in Pineapple Stump Material With and Without Beetles
(Tabulated values give the estimated per cent remaining.)

Time in Weeks	Without Beetles	With Beetles
0	4.83%	4.83%
2	8.43	5.99
4	2.89	1.65
6	1.56	0.55
8	0.64	0.37
12	0	0

The increased loss of alpha cellulose due to the presence of beetles indicates that there may be cellulose decomposing organisms in the intestinal tract of the beetles similar to those in the case of the intestinal flora of termites which were investigated by Cleveland (3 and 4). There is, however, the possibility that mere presence of the beetles may so alter the decomposing stump that it is more readily inoculated with the organisms which decompose cellulose.

(e) ***Decomposition of sugars as influenced by the presence of Carpophilus beetles.***—The sugars which are present at any stage of decomposition in pineapple stump material are not only the original sugars but also those which appear from the hydrolysis of the starches, pentosans and cellulose. The sugars present at various stages of decomposition are shown in Table XIII and Fig. 8. There is an immediate increase in the amount of sugar as soon as decomposition starts but this is lost in a very short time so that no sugars are found at the end of three months of decomposition. The presence of the beetles tends to accelerate the decomposition of the sugars at all stages of decomposition. The differences shown are probably significant since they are based on the analysis of composite samples of thirty stumps.

There is no practical significance from the increased sugar losses since the sugars are not the fraction of the pineapple plant which hinders the decomposition of the materials in the field. Sugars are lost very early and are gone long before the more resistant fractions even begin to decompose.

(f) *Decomposition of starch as influenced by the presence of Carpophilus beetles.*—The starches in pineapple stumps are readily lost during decomposition. The influence of the beetles is not marked as is shown in Table XIV and Fig. 9 At later stages of decomposition there seems to be an actual inhibiting effect due to the presence of the beetles. No very obvious reason for this hindering influence is known, though it seem to be consistent after decomposition has proceeded for a month.

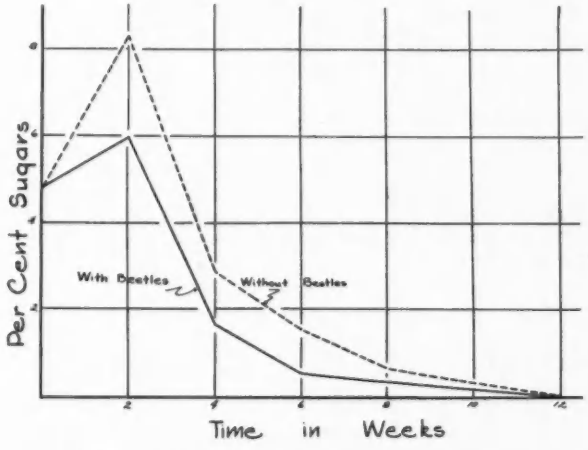

FIG. 8. Decomposition of sugars in pineapple stumps.

The decomposition of starch is dependent on the presence of abundant moisture and it is possible that the aeration of the stumps due to the activity of the beetles may lower the water content to the point of actually hindering the decomposition of the starch. No measure of the water content of the stumps was taken, so this cannot be demonstrated. A small percentage of the starch still remains after the stumps have decomposed for three months, but this is insignificant in comparison to the other fractions.

(g) *The influence of Carpophilus beetles on the fats present in pineapple stumps during decomposition.*—The fats and waxes present in pineapple plants during decomposition represent a complex when measured in terms of the ether soluble extract. There are not only the complexes of fats and waxes of the original material, but also the fats and fatty materials which are synthesized by organisms of decomposition. In all cases this ether soluble extract represented less than 1%

of the total stump material. The results are shown in Table XV and Fig. 10. The decomposition of fatty substances in the soil is not a rapid process according to Waksman (24) and the differences shown in favor of the beetles may be more apparent than real. The trend of

TABLE XIV

Decomposition of Starch in Pineapple Stump Material With and Without Beetles
(Tabulated values give the estimated per cent remaining.)

Time in Weeks	Without Beetles	With Beetles
0	42.32%	42.32%
2	18.84	20.20
4	12.14	12.33
6	8.12	4.78
8	3.42	2.10
12	1.18	1.66

the decomposition of fats in the samples without beetles indicates that there is the expected momentary increase of fats due to synthesis of fats by micro-organisms. In the samples with beetles present, there is an immediate slight rise and then a continued falling off of the fatty

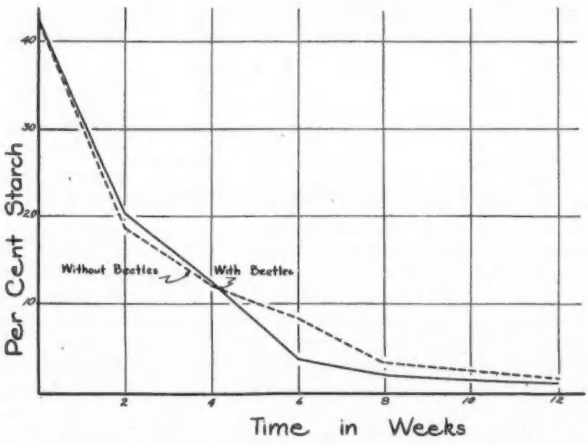

FIG. 9. Decomposition of starch in pineapple stumps.

fraction. The most obvious explanation for this is that the beetles leave the stumps and die elsewhere taking with them the fats that they have accumulated in their tissues. Thus the apparent loss of fats is not a real one represented in terms of decomposition of those fats. The

fats of pineapple stumps are not present in sufficient quantities to be any very important factor from the field standpoint.

(h) *Discussion of the results of the studies on decomposition.*—The influence of Carpophilus beetles on decomposition of pineapple stump material can be definitely measured and it has been demonstrated that

TABLE XV

Decomposition of the Ether Soluble Substances in Pineapple Stump Material With and Without Beetles

(Tabulated values give the estimated per cent remaining.)

Time in Weeks	Without Beetles	With Beetles
0	0.82%	0.82%
2	0.66	0.86
4	0.72	0.76
6	0.78	0.60
8	0.55	0.44
12	0.34	0.32

the beetles do increase decomposition in its earlier stages. The more resistant fractions, which are the most important from the practical standpoint, are apparently speeded but little in their decomposition. The gains in the rate of decomposition which are made in the earlier

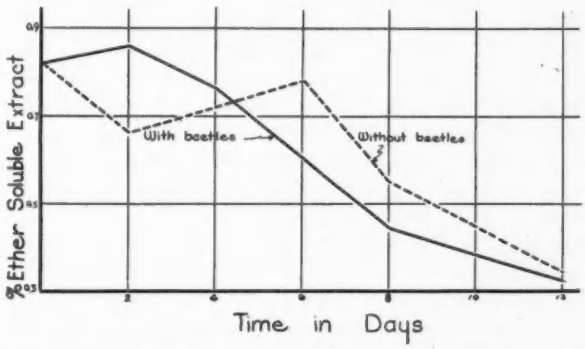

FIG. 10. Decomposition of fats and waxes in pineapple stumps.

stages, when measured on the basis of dry weight losses, are very nearly lost at the end of three months of decomposition. The analysis of the various fractions does not indicate that there is any significant difference in the rates of decomposition of any of the fractions.

Considered from the field aspect there is no benefit to be expected from having the beetles present to hasten the decomposition of trash which remains in the field after the field is removed from production.

The field man is concerned with the decomposition of the total trash rather than with any of its fractions, and beetles are shown to be unable to hasten the process when it is considered as a whole.

XIII. SUMMARY AND CONCLUSIONS

1. Six species of Nitidulidae are found in the pineapple fields of Hawaii. Of these, *Carpophilus humeralis* (Fab.) and *C. hemipterus* (L.) are the most important with *C. maculatus* Murr, and *Haptoncus ocularis* (Fairm.) assuming a minor role. *C. dimidiatus* and *Haptoncus mundus* Sharp are species of relative rarity.

2. The appearance of these species in abundance seems to be related to the peculiar conditions of pineapple culture which furnish suitable environments for the increase of these species.

3. None of the species is capable of inflicting primary injury either directly or as vector of a disease of any part of the pineapple plant. Butt rot, the one possible exception, was not investigated.

4. The economic importance of the beetles is mainly as a nuisance in the canneries where special precautions must be taken to prevent the beetles from getting into the cans of fruit.

5. Both of the important species are shown to have a high potential of reproduction and a short immature period as compared to the length of life of the adult.

6. There is a tendency for *Carpophilus hemipterus* to be the more abundant in the early stages of decomposition and to be replaced by *C. humeralis* at later stages.

7. The theoretical proposition of Volterra of any number of species competing for the same food cannot be applied to the present field study since the numbers of the two major species which will be present is controlled by mobility and migration factors rather than factors of reproduction and voracity.

8. The influence of the Nitidulid beetles in speeding decomposition can be measured definitely in terms of dry weight loss. The increase which is evident in the early stages is lost in the later stages.

9. The presence of the beetles gives no practical benefit in hastening the decomposition of trash in pineapple fields.

10. Chemical determinations of the fractions of materials remaining in decomposing pineapple stumps indicate that no fraction is speeded in its decomposition to the detriment of the other fractions.

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BOOK NOTICES

A CONTRIBUTION TO A BIBLIOGRAPHY OF THE DESCRIBED IMMATURE STAGES OF NORTH AMERICAN COLEOPTERA, by J. S. WADE. (Mimeograph), pp. 1–114. September, 1935.

No statement is given as to whether this is a private publication by the author or is by the U. S. Bureau of Entomology and Plant Quarantine. It carries its own index as all matter, except a short introduction, is a list of species arranged alphabetically, first by genera, second by species in each genus.

This is a substantial help in library work necessary to such a subject. The last similar publication was one by Beutenmüller in the Journal of the New York Microscopical Society in 1891. The author knows libraries and entomological literature and has already given us other very useful bibliographies on entomological subjects. Unfortunately, entomology is not well supplied with competent bibliographers. With our own university department staff reference work becomes burdensome because of the scattered literature. All such efforts as this of Mr. Wade's are widely appreciated, an appreciation that is not so obvious in the mimeographing of such a useful work.—C. H. K.

AN ABRIDGED CATALOGUE OF CERTAIN SCUTELLEROIDEA (PLATASPIDAE, SCUTELLERIDAE, AND PENTATOMIDAE) OF CHINA, CHOSEN, INDO-CHINA, AND TAIWAN, by WILLIAM E. HOFFMAN. Lingnan University, Canton, China, Science Bulletin, No. 7, pp. 1–294. 1935.

This is apparently a very useful work for Hemipterists. After an elaborate introduction by the author, discussing the problems involved, pages 9 to 177 are devoted to the catalogue proper. Pages 180 to 186 contain a list of species treated. Pages 187 to 257 carry an annotated bibliography of the subject. Following the bibliography are Appendices on faunal regions and geographic distribution of the species discussed. It includes also a list of place names, pages 276–285, with their location politically and zoogeographically. The volume closes with an index to all species and synonyms. Thus this work is a well planned key to the literature on the list of species involved. It is well printed on good paper.

—C. H. K.

CICADELLIDAE OF HAWAII, by HERBERT OSBORN. Bernice P. Bishop Museum, Bulletin 134, pp. 1–62, figs. 1–27. 1935.

This is a taxonomic monograph of the leafhoppers of the Hawaiian Islands. The twenty-five or more new species are illustrated. Two new genera are described, one with two species and one monotypic. Nine other small genera of one to five species each occur but the great number of species (fifty-nine) fall in one endemic genus, Nesophrosyne, the species of which are largely limited to native plants.

We give this notice to call attention to the peculiarity of the Hawaiian fauna. In zoogeography it is of the oceanic island type. The islands are very old geologically and due to their great isolation few faunal stocks have been able to reach the islands from surrounding continents. These early stocks during this long period of isolation, perhaps since the early or middle Tertiary, have evolved into the numerous but closely related species characteristic of the Hawaiian fauna. Mixed with these are always a scattering of small genera of more recent introduction. These early introductions with the later evolution of numerous endemic species usually show relation to the Asiatic fauna while later introductions may be related to the Americas. This is singularly true in the Odonata. The literature on distribution is full of articles on the Drepanidae (birds) and Acha-

tinellidae (tree snails) of the Hawaiian Islands which are outstanding examples of the development of groups in isolated territory. The birds have evolved to numerous generic forms but the majority of the other groups are usually considered as great genera of closely related species.

In the case of the leafhoppers, Professor Osborn points out that we are not yet able to say whether Nesophrosyne originated in Asia or America. Some of the recent introductions have been serious pests.

This monograph is one example of the excellent work in entomology which is now being done by the Bishop Museum, the Hawaiian Entomological Society and the laboratories devoted to work on the pests of cane and pineapples.—C. H. K.

INSECT PHYSIOLOGY, by V. B. WIGGLESWORTH, pp. i-x and 1-134; 13 illustrations, 1934. Published by Methuen and Co., Ltd., 36 Essex St., London, W. C., England. Price 3s. 6d. net.

Our previous summaries of insect physiology have been in volumes in which morphology has had the greater emphasis. This book minimizes structure. It gives just enough anatomy to make physiological processes clear. Wigglesworth, known to entomologists for his many papers on insect anatomy and physiology, has given us a review of the very latest researches as is shown by the Bibliography of 297 items, few of which date back of the year 1925. However, it is stated in the Introduction that over 2,000 publications were studied.

The subject matter is divided as follows: Chapter I, Integument; II, Respiration; III, Circulatory System and Blood; IV, Digestion; V, Excretion; VI, Nutrition and Metabolism; VII, Reproduction and Growth; VIII, Nervous System, Sense Organs and Behavior.

The present volume is priced within the reach of every entomologist, is well bound and beautifully printed.—C. H. K.

COMPARATIVE PSYCHOLOGY, A COMPREHENSIVE TREATISE, by CARL J. WARDEN, THOMAS N. JENKINS AND LUCIEN H. WARNER. Vol, I, PRINCIPLES AND METHODS, pp. i–x, and 1–506, 141 text figures. 1935. Published by the Ronald Press Co., 15 East 26th St., New York City. Price, $4.50.

This is the first volume of a three-volume work. The titles of the forthcoming volumes will be "Plants and Invertebrates," and "Vertebrates." The point of view and treatment of the subject matter in Volume I is consistent with the following statements in the introduction:

"The aim of the present volume is to provide the student with the proper background for an understanding of the survey of plant and animal behavior to be covered in the two later volumes. The first four chapters offer a broad historical and theoretical approach to the viewpoint and problems of comparative psychology. The next two chapters * * * attempt to systematize * * * the methodology of the science. The final chapter comprises a comparative survey of the structure and function of the receptive, transmissive, and reactive mechanisms of living organisms."

In more detail the titles of the chapters are as follows: Chapter I, Development of Modern Comparative Psychology; II, The Natural Science Viewpoint in Biology; III, Biological Foundations of Comparative Psychology; IV, Classification and Analysis of Behavior; V, Methods of Testing Receptive Capacities; VI, Methods of Testing Reactive Capacities, and VII, Comparative Morphology and Physiology of Organisms. The volume contains also a closely selected Bibliography of sixty-seven pages, and author index and a subject index.

Several zoologists interested in studies of animal behavior have looked this volume over at the request of the present writer and are pleased with its sound zoological point of view and its well organized treatment of the subject.

Figures 11 to 58 show various types of apparatus used in the study of behavior. Much of this material has a specific application to the study of vertebrates but is suggestive for work with insects. The whole (Chapters 5 and 6) is so chosen

and organized as to give the fundamental principles involved in the various methods of experimentation.

We recommend this book for all those interested in insect behavior. It appears to be one of the best general reviews of the subject of behavior from the point of view of the experimental zoologist.

The book is well bound, is on good paper and is printed in a widely spaced type that makes for easy reading. The illustrations are reproductions from the literature and in various cases are not up to the quality of the other features of the work.—C. H. K.

SOME LABORATORY EXERCISES IN INSECT PHYSIOLOGY, by J. FRANKLIN YEAGER. (Mimeograph), pp. 1–102, 14 figs. Iowa State College Printing Department, Ames, Iowa. Price, 85 cents, post-paid.

Professor Yeager is a physiologist who has turned to a study of insects. The volume is a detailed set of thirty instructions for the set up and interpretation of as many experiments in insect physiology. Some of these are: I, General Observations of the Living Insect; II, The Coagulation of Insect Hemolymph; VIII, Circulation in the Insect Wing; XI, Phagocytosis by Hemolymph Cells; XIII–XVI, Mechanics of the Insect Digestive Tract; XVII–XXI, Digestive Enzymes; XXII, Alimentary Absorption; XXIV–XXV, Excretion: Malpighian Tubules; XXVI–XXIX, Functions of the Insect Nervous System, and XXX, Detection of Chitin.

Following the body of the text is a list of 97 references to serial literature and a list, four pages long, of books on the various physiological problems treated in the volume.

This is the first laboratory guide of its kind, that on insect physiology, and every teacher of entomology will certainly welcome it. For the fraternity of entomologists we thank Professor Yeager for "breaking the ice" in this new area of the laboratory instruction in insect physiology.—C. H. K.

OMISSIONS AND ERRORS

NOTICE TO AUTHORS.—Beginning with Volume 28 (1935), the Annals of the Entomological Society of America will accept Corrections (*Omissions* and *Errors*) of articles which have appeared in its pages. These will be collected and printed at the end of the annual volume (December issue). They will be indicated in the annual table of contents and in the index.

Corrections will be limited to critical omissions and serious errors. Manuscript for such should be in the hands of the Editors by the twentieth of November to be included in that year's volume. THE EDITORS.

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Page 20, fig. 14, legend:

For "Liassophilidae" and "Liassophlebiidae," read "Liassophila" and "Liassophilidae".

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